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Invading species spreading biological pollution

Book chronicles worldwide travels of flora, fauna and bugs

By David Briscoe
The Associated Press

WASHINGTON — An alarming breed of biological pollution, spreading around the world, may be sitting quite prettily in your backyard. Exotic species of plants, bugs and animals, carried across borders intentionally or by accident, pose new dangers in places they don't belong.

Asian tiger mosquitoes are biting Americans, and termites from Taiwan are eating American houses. An Atlantic jelly fish is destroying fisheries in the Black Sea. The South American water hyacinth is shrouding lakes in China and Africa. Tree snakes from Papua New Guinea are gobbling up bird species on the faraway island of Guam.

Like global commerce, species are traveling faster and farther than ever. They swim in the ballast of supertankers, slither up into the wheelwells of jetliners, and sometimes bore into valuable artifacts.

Environmentalists call it "smart pollution," because new species can quickly evolve to dominate and sometimes destroy native plants and animals.

Environmental researcher Chris Bright says it's the second greatest threat to the biological diversity of the planet, next to the loss of habitat.

"Even the worst chemical spills are dumb. They cannot reproduce and they dissipate over time. But smart pollution proliferates and spreads," said Bright, author of "Life out of Bounds," published this weekend by the nonprofit environmental research group Worldwatch Institute and W.W. Norton & Co.

"Invasion itself is an ancient process," Bright said. "What's new is that the integration of the global economy is spreading more and more creatures around.

Some invaders are well known: the pipe-clogging zebra mussel, the bird-devouring brown tree snake or the landscape-smothering kudzu vine. Most are more subtle and can be found in backyard gardens or public parks.

"We can look right at it. It can be looking us back in the face, and we don't even see it," Bright said.

About half of the 300 serious plant pests in North America were first grown in gardens, says the report.

The foreign invaders of various lands and waters include:

■ Water hyacinth from South America, originally imported as a pool ornament and which now covers whole lakes in the United States, Africa and southern Asia.

■ East Asian longhorned beetles that have turned up recently in New York City and Chicago, where they bore into maple and other trees.

■ The Asian tiger mosquito, which can carry at least 17 different viruses, some of them fatal, and has turned up in such scattered places as Brazil, Nigeria and, last fall, Peoria, Ill.

Future dangers also lurk.

The book warns of the danger of yellow fever traveling from Kenya to India, where the population "is wholly unvaccinated against it," the import of foreign raw logs into the U.S. Pacific Northwest which could bring in hundreds of new pests.

The book suggests strengthening international treaties, re-engineering ship ballast water systems that carry foreign plants and creatures, developing international monitoring systems on invasive species, stopping the intentional introduction of exotic species and promoting the use of native species in gardens around the world.

IOP TODAY 11 AM 'TIL 7 PM

SUPER

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Ecological Applications, 3(4), 1993, pp. 558–560

SCIENCE AND THE MANAGEMENT OF NATURAL RESOURCES[1,2]

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We are in full agreement with Ludwig et al. (1993) that scientific and technological progress will not, in themselves, lead to sustainable development of resources. One can hardly hope for rational management of resources in a world in which many (if not most) politicians, managers, and economists still believe that resources are either infinite in extent or infinitely substitutable (Ehrlich 1989) and where social dynamics generally lead to overexploitation regardless of beliefs. We agree also with the thrust of their argument that more scientific knowledge is not the main key to sustainable management of our planet's resources.

We can hardly fault the Ludwig team's (1993) prescriptions either, such as taking action before scientific "consensus" is achieved. After all, social dynamics often prevent action even when there is consensus (which is not necessarily unanimity) among scientists. Consider, for example, the "World Scientists' Warning to Humanity," circulated by the Union of Concerned Scientists in 1992, and signed by a majority of living Nobel laureates in the sciences. It called, among other things, for halting growth of the human population, reducing greenhouse gas emissions, and protecting biodiversity. Despite that warning (and many others representing the consensus of environmental scientists in the past), the threats of continued overpopulation, global warming, and extinction are hardly appreciated by the public. That failure can be traced largely to a media penchant for inflating the views of tiny minorities to give the appearance of controversy. A few scientists can always be found who, sometimes because of legitimate scientific concerns, but more often because of political pressures or yearning for public attention, give ammunition to those promoting their private interests at society's expense.

On the other hand, Ludwig et al. (1993) prove their own assertion true, that "the judgement of scientists is often heavily influenced by their training in their respective disciplines." Much of the experience in fisheries is not generalizable to the management of resources most relevant to sustaining human civilization. These include soil, freshwater, forests, atmospheric composition, and some level of biodiversity (see Daily and Ehrlich 1992) for which sustainable use/destruction rates are at least approximately known and for which more research does promise a substantial reduction of uncertainty.

We disagree with the implication of Ludwig et al. [1993:proposition (iii)] that the complexity of bio-

[1] Manuscript received 2 June 1993.
[2] For reprints of this Forum, see footnote 1, p. 545.

sequences may not lead to effective steps toward amelioration. This is amply demonstrated in the rapid degradation of potentially productive land, a problem that currently afflicts nearly 20% of Earth's vegetated land (WRI 1992). But the agricultural situation is little understood and low on the agenda of most educated people and world leaders (Ehrlich et al. 1993).

Only when a special mix of social conditions exists may the combination of perception and mechanistic understanding trigger strategic assessment (usually interdisciplinary) and a significant social response. The social activism of the 1960s, certainly intensified by the Vietnam War, and the environmental movement (given impetus by the publication of Rachel Carson's *Silent Spring* in 1962) set the stage for passage of relatively strong environmental legislation in the U.S.

Not only is the special mix of conditions difficult to generate, but its establishment is difficult to forecast. The conditions seem to include, among other things: a relatively simple solution at hand (involving few parties, little expense, and little or no foreseen short-term change in lifestyle); a clearly perceived high cost associated with inaction; a charismatic, visionary leader; and favorable (short-term) economic conditions. When most of these ingredients are present, and society is deciding to take action, strategic assessment becomes relevant and the availability of the best possible scientific information becomes critical.

Good science is thus important at each stage. It can document and quantify the problem, making it more difficult for countervailing forces to claim it is nonexistent. Good science, and often it alone, can properly pinpoint causes and project consequences. And, collaboration between natural and social scientists can provide decision makers and the general public with clear evaluations of options, costs, and benefits to guide social action. They can also offer advice on which courses they think best, especially on critical nonscientific issues dealing with how "fail-safe" courses of action should be, and how to deal with zero–infinity problems and thresholds. In that capacity, however, they must shed any mantle of impartiality and simply speak as well-informed citizens, which we believe they have an obligation to do.

Acknowledgments

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GREED, SCALE MISMATCH, AND LEARNING[1,2]

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Ludwig et al. (1993) make an important criticism of the idea of sustainable exploitation of resources: without an adequate grasp of the human dynamics that drive exploitation, there can be no adequate understanding of how sustainability could be achieved or maintained. Indeed, it is not obvious that a regime of stable use exists under any set of social arrangements, a point underscored by the history cited by Ludwig et al. (1993). History holds other lessons as well, and in this note I suggest two ways to advance beyond Ludwig et al.'s cautions: first, by considering environmental problems as driven by mismatches of scale between human responsibility and natural interactions; and second, by emphasizing the central roles of learning and conflict as means of correcting human error in the natural world.

Ludwig et al. (1993) cite examples from fisheries, forestry, and irrigated agriculture, demonstrating that technocratic ideas such as maximum sustainable yield may be much more difficult to put into practice than analysts or policy makers have assumed. It may be

[1] Manuscript received 2 June 1993.
[2] For reprints of this Forum, see footnote 1, p. 545.

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DEVELOPING ECOLOGICAL RESEARCH THAT IS RELEVANT FOR ACHIEVING SUSTAINABILITY[1,2]

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In their excellent recent article, Ludwig et al. (1993) accurately identify many of the underlying reasons for nonsustainable resource use. They conclude by enumerating five basic principles of effective management: (1) include human motivation; (2) act before scientific consensus is reached; (3) rely on scientists to recognize problems but not to remedy them; (4) distrust claims of sustainability; and (5) confront uncertainty. I agree, in general and wholeheartedly, with all of these principles. My only quibble is with their assertion, included as an expansion of principle 4, that basic ecological research on the topics identified in the Sustainable Biosphere Initiative (SBI, Lubchenco et al. 1991) is irrelevant to achieving sustainability. A unique feature of the SBI document was that in identifying the research needs for a sustainable biosphere, a group of ecologists pinpointed many areas of research that go well beyond the boundaries of traditional ecology and require a broad, interdisciplinary collaboration. Narrow, traditional ecological research is not relevant by itself, but the broad interdisciplinary research recommended in the SBI can be. But in order for the recommended SBI research to actually be relevant, some additional major changes in how we view science in general, and especially the linkages between science and environmental policy, are going to be needed.

As Ludwig et al. (1993) point out, one of the primary reasons for the problems with current methods of environmental management is the issue of scientific uncertainty, not just its existence, but the radically different expectations and modes of operation that science and policy/management have developed to deal with it. If we are to solve this problem, we must understand and expose these differences and design better methods to incorporate uncertainty into the policy making and management process.

To understand the scope of the problem, it is necessary to differentiate between *risk* (which is an event with a *known* probability, sometimes referred to as statistical uncertainty) and *true uncertainty* (which is an event with an *unknown* probability, sometimes referred to as indeterminacy). Most important environmental problems suffer from true uncertainty, not merely risk.

Science treats uncertainty as a given, a characteristic of all information that must be honestly acknowledged and communicated. Over the years scientists have developed increasingly sophisticated methods to measure and communicate the uncertainty arising from various causes. It is important to note that the progress of science has, in general, uncovered *more* uncertainty rather than leading to the absolute precision that the lay public and some policy makers often mistakenly associate with "scientific" results.

The scientific method can only set boundaries on the limits of our knowledge. It can define the edges of the envelope of what is known, but often this envelope is very large and the shape of its interior can be a complete mystery. Science can tell us the range of uncertainty about global warming, the potential impacts of toxic chemicals, or the possible range of fish population dynamics, and maybe something about the relative probabilities of different outcomes, but in most important cases it cannot tell us which of the possible outcomes will occur with any degree of accuracy.

Our current approaches to environmental management and policy making, on the other hand, abhor uncertainty and gravitate to the edges of the scientific envelope. The reasons for this are clear. The goal of policy is making unambiguous, defensible decisions, often codified in the form of laws and regulations. While legislative language is often open to interpretation, regulations are much easier to write and enforce if they are stated in clear, black and white, absolutely certain terms.

As they are currently set up, most environmental regulations, particularly in the United States, *demand certainty* and when scientists are pressured to supply this nonexistent commodity there is not only frustration and poor communication, but mixed messages in the media as well. Because of uncertainty, environmental issues can often be manipulated by political and economic interest groups. Uncertainty about global warming is perhaps the most visible current example of this effect. In order to rationally use science to make policy we need to deal with the whole envelope of possible futures and all their implications, and not delude ourselves that certainty is possible.

The "precautionary principle" is one way the environmental regulatory community has begun to deal with the problem of true uncertainty. The principle states that rather than await certainty, regulators should

[1] Manuscript received 2 June 1993.
[2] For reprints of this Forum, see footnote 1, p. 545.

nize the edges and worst cases, but do not rely on them to remedy the problems themselves. Research needs to be "policy-linked" and "edge-focused."

4) Distrust claims of sustainability and confront uncertainty by shifting the burden of proof from the public to the parties that stand to gain from resources use. One mechanism for doing this is through the use of "environmental assurance bonds" that require resource users to post a bond large enough to cover the worst case damages with the potential for refund if the damages are less (Costanza and Cornwell 1992).

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ACHIEVING SUSTAINABLE DEVELOPMENT THAT IS MINDFUL OF HUMAN IMPERFECTION[1,2]

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"Uncertainty, resource exploitation, and conservation: lessons from history," by Donald Ludwig, Ray Hilborn, and Carl Walters (1993) is a cry from three people who are convinced that "sustainable development" is an "illusion," and that scientists, especially ecologists, are the principal perpetrators of this illusion. To probe the authors' discomfort more deeply, let us distinguish two kinds of illusions. Might sustainable development be an illusion, call it Type S, rooted in scientific understanding? A perpetual motion machine is a Type S illusion. Or might it be an illusion rooted in human nature, call it Type H? Modern Soviet Man, sacrificing personal welfare for the general good, turned out to be an illusion of Type H.

At the level of fisheries management, the authors implicitly argue that "sustained yield" (a necessary component of sustainable development) is also an illusion. Sustained yield would be an illusion of Type S, if substantial fishing inevitably drives the corresponding fishery to extinction. I infer that the authors believe that sustained yield is an illusion not of Type S but rather of Type H, which would be the case if every human institution invented to manage fishing were to drive the corresponding fishery to extinction. To prove the authors wrong, that is, to find that sustained yield is not an illusion at all but an attainable achievement, one would have to confirm that the population dynamics of fish are robust and that institutions for the management of fishing can be designed to operate indefinitely within that robustness.

As an outsider, I am surprised by the negative view of the role of ecological science in achieving sustainable outcomes: surely the progress in restricting whaling and poaching has been abetted by population biology.

The distinction between Type S and Type H illusions is crucially important when the argument is generalized to global sustainable development. For the sake of discussion, let us agree that what is to be evaluated are patterns of global economic activity on this planet for at least the next few hundred years. Let us further agree that for a pattern to be judged consistent with sustainable development it must meet two constraints: (1) within a small fraction of the total time under consideration (say, 50 yr out of 500 yr) nearly all of the earth's human beings achieve a lifestyle of considerable vigor and quality, and (2) during the time under consideration the survival of the human population and the populations of nearly all other species sharing this planet is not put in jeopardy as a result of life-threatening changes in the natural environment. If sustainable development so defined is an illusion of Type S, then, in

[1] Manuscript received 7 June 1993.
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Introduced Fish Section

of the American Fisheries Society

National Invasive Species Act of '96 to be Reauthorized

INSIDE

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President's Corner

by Eric Hallerman

I am pleased to take the reins of leadership from Past President Neal Foster. Thanks, Neal, for your efforts on behalf of the Section. I look forward to a busy year, filled with interactions with aquatic scientists, both inside and outside the Introduced Fish Section (IFS).

Section business. I encourage every IFS member to actively participate in Section business. Perhaps the most important action you can take is to use the ballot in this newsletter and vote. First of all, we must move to renew the leadership of the Section. We have two fine nominees for the office of President-Elect [see candidate's statements]. Choose one, or fill in the name of a write-in candidate.

Also, we must reach decisions on two issues not decided at the annual business meeting in Dearborn [see Minutes]. We seek your vote on these two issues:
- The major expense faced by the Section is production and mailing of the Newsletter [see Treasurer's statement]. A disproportionately large portion of the mailing expense is postage to international members. We ask our international colleagues whether they would be willing to add an additional US$2 to their annual dues to support the high cost of mailing.
- The Skinner Memorial Fund supports the travel of outstanding fisheries students to the AFS annual meeting. With interest rates rather low of late, just a few students' travel could be supported this year. The solution to this problem is to increase the Fund's endowment. The AFS Education Section is challenging all AFS subunits to contribute to the Fund. Since our Section's budget is limited, pursuant to the decision reached at our annual meeting, we ask the IFS membership to ratify a token $100 donation to the Skinner Memorial Fund, thereby investing in the future of our profession.

The AFS Professionalism Committee suggests the possibility of the Section starting ots own awards program. Discussion at the annual IFS business meeting showed interest in establishing awards for students, for professionally established IFS members, and for outstanding individuals outside of the Section or of AFS. Should there be sufficient interest, I will name an ad hoc committee to develop a detailed proposal for an IFS awards program. Anyone interested in serving on such a committee, please contact me.

At the IFS business meeting, we gave IFS ex-President Denny Lassuy the go-ahead to develop a symposium for the AFS annual meeting next August on the role of public and private aquaria. Other IFS members also may propose symposia for Section sponsorship. You'll have to move quickly, as the deadline for submission of proposed symposia is December 23 [see p. 27 in the September issue of Fisheries]. The Section leadership will need, say, two weeks to review any proposal and consider Section sponsorship - it would be best to involve us as early as possible in your planning process.

Passage of NISA. The Non-Indigenous Aquatic Nuisance Prevention and Control Act of 1990 was our nation's response to the zebra mussel invasion, aimed at minimizing the likelihood of future accidental introductions. Reauthorization of the Act was emobodied in House and Senate bills for a National Invasive Species Act. As President of IFS and follwing feedback from other IFS officers, I submited written testimony supporting passage of NISA [see related story]. After much legislative wrangling, NISA was passed by both houses of Congress, and is expected to be signed into law by the President.

Communications. Perhaps my key agenda item as Section President is improving communication within IFS. I feel that improved communication will enhance both the cohesivenss and effectiveness of the Section. So, send me your e-mail address (ehallerm@vt.edu) - I'll add you to my IFS nickname file, and you'll share in Section discussions. Within the next few weeks, I'll organize a listserver for the Section, which we can all use for sharing information and discussions of issues of IFS interest.

After the listserver is up and running, I will organize an IFS homepage on the World Wide Web. I anticipate that the homepage will display hotlinks to relevant AFS position statements, recent news items, and other WWW sites (send me suggestions), as well as the names and e-mail addresses of Section officers. I hope that a Section presence on the Internet will attract new members and foster informed discussion of issues posed by introduced aquatic species.

Newsletter editors. Publication of this particular newslettter was a cooperative effort by outgoing Editor Don Baltz and incoming Editor John Cassani. Thanks, Don, for the many fine newsletters you've published over the last five years. Thanks, John, for taking the reins.

In closing this message, I hope my term as President will prove stimulating to the IFS membership. Let's interact.

From the Editor

by Don Baltz

As editor, I have received several requests from members and non-members for past issues of the newsletter. Often I have been able to send copies of recent issues, but have been unable to fill requests for older issues. The Section should have an archive, so if someone has a complete set, please let Eric Hallerman know. If former newsletter editors still have digital copies of past issues, they would be especially useful for distribution on the information highway in connection with IFS's pending homepage and listserve.

I want to thank all of you who contributed abstracts, clippings, and correspondence to the newsletter over the years and ask that you continue to support IFS by bringing newsworthy items to the Section's attention. Now it is my pleasure to turn the editorship over to John Cassani.

Senate Hearing the National Invasive Species Act (NISA) of 1996

.... Correspondent: Trudy Harlow [Intergovernmental Affairs, Office of Outreach, 119 National Center, Reston, VA 21092]

On September 19, a panel of experts from scientific, commercial, and regulatory interests gave testimony to the Senate Subcommittee on Drinking Water, Fisheries, and Wildlife. Senate bill 1660 sponsored by Sen. John Glenn (D-OH) reauthorizes the Non-Indigenous Aquatic Nuisance Prevention and Control Act of 1990 which mandates the discharge of a ship's ballast water before entrance into the St. Lawrence Seaway.

The intent of this bill (S. 1660) is to prevent the further introduction of non-native aquatic species into the nation's water systems. The bill stipulates that the same measures be taken in all other waters of the United States, but on a voluntary basis. The Coast Guard will regulate and record the efforts designed by this bill and, if a general agreement is added to the bill, the Coast Guard will produce a report to the Senate after two years reporting on the effectiveness and compliance of these actions. In addition to these measures, the bill authorizes additional coastal research in the Pacific Northwest addressing the problem of invasive species.

The discharge of ballast water is blamed for the introduction of non-native species such as the zebra mussel which have the potential to become ecological and economic nuisances. According to Senator Glenn, a new species invades San Francisco Bay every twelve weeks. The potential for the invasive species to threaten major fisheries is a grave concern shared by those who testified. Before the testimony was given, Senators Reid (D-NV) and Baucus (D-MT) expressed concerns that terrestrial and land-locked ecosystems are in danger similar to that affecting the maritime industry. The chair of the committee, Senator Kempthorne, assured the panel that this bill is one of importance that will be acted upon expeditiously.

In attendance at today's hearing were Senator Kempthorne, Chair, and Senators Baucus, Reid, Glenn, and Bennett. Testimony was heard from: Rowan Gould of the U.S. Fish and Wildlife Service, Commander Rich Gaudiosi of the U.S. Coast Guard, Dr. James Carlton of the Williams College Mystic Seaport Maritime Studies Program, Ann Swanson of the Chesapeake Bay Commission, Steve Hall of the Association of California Water Agencies, and Joseph Cox of the U.S. Chamber of Shipping.

For more information contact the Senate Subcommittee on Drinking Water, Fisheries, and Wildlife at 202/ 224-9134.

House Passes NISA September 25, 1996

.... Correspondent: Allegra Cangelosi

The House Committees of jurisdiction completed work late Monday on a "Managers' Amendment" for House floor consideration Tuesday. The Managers' Amendment is a rewrite of HR 3217 with changes requested by interest groups and regional delegations since mark-up of the legislation in early September. These changes fall into four basic categories:

1. Changes related to the ballast management program (addressing concerns of the maritime industry via Congressman Young, Senator Lott, and others on the Senate Commerce Committee);
2. Changes to related to California (addressing concerns of California members in the House and Senate);
3. Changes related to the research component of the bill, generally (addressing concerns of the House Science Committee);
4. Other technical changes.

The maritime-related changes track those outlined as components of the compromise reached by Senator Glenn and maritime players, except that the bill gives no assurance that other actions will not be required of vessels utilizing the safety exemption. In summary, the maritime-related additions are provisions which: a) clarify the sole discretion of the Master in making the safety call; b) assure non-discrimination with respect to vessel flag; c) assure consistency with any international regulations that may be approved by the US; and d) include a reporting requirement on the Coast Guard and postpone the advent of any regulations until 6 months following the completion of the report.

In addition, in partial response to an oil industry (via Young and others) demands, the TAP tankers which carry crude oil coastwise into Alaska are exempt from any ballast management regulations that may be promulgated to enforce the voluntary guidelines.

California-related changes include appointment of a San Francisco Estuary Project representative to the ANS Task Force, authorization of $750,000 for research on San Francisco Bay and Estuary (in addition to the $500,000 specifically allocated for Pacific Coast research, and the $2 million provided for ecological and ballast discharge surveys nationally, including in California).

Changes related to the research component of the bill include the addition of a provision directing the Task Force to conduct an ecological and ballast discharge survey on the Columbia River. The bill also now directs regional research dollars to N0AA for distribution in specific regions for competitive grants. The national clearinghouse of info is now to be conducted in consultation "and cooperation" with the Smithsonian (rather than just consultation).

The Managers' Amendment was approved by the House Tuesday afternoon. The Senate Commerce Committee has placed a hold on the legislation pending assurances that the maritime industry's needs have been met.

If you would like a rundown of the other technical changes, or have any questions, please contact me at 202-544-5200.

IFS NISA Senate Testimony

The Non-Indigenous Aquatic Species Prevention and Control Act of 1990 (ANS Act) was a major piece of federal legislation aimed at controlling accidental release of non-indigenous aquatic species. The Act had a five-year sunset clause and needs to be reauthorized. Efforts were made in both houses of Congress to adopt a reauthorization, the National Invasive Species Act of 1996 (NISA). Like the ANS Act, Senate bill S. 1660 largely addressed Great Lakes issues posed by the zebra mussel. House bill H.R. 3217 was broader, extending the scope of the ANS Act to all coasts. A hearing on the Senate bill was held by the Environment and Public Works Committee on September 23. Introduced Fish Section President Eric Hallerman submitted written testimony, which appears below.

H.R. 3217 was passed by the House of Representatives on September 24. Amendments to S. 1660 were drafted to make the bill acceptable to virtually all Senators. As the Congressional session ran down to the wire, the House adopted a bill, H.R. 4283, whch was identical to S. 1660. One of the Senate's last actions before adjournment was adoption of S. 1660, paving the way for the President's signature and enactment into law.

Testimony of Eric M. Hallerman for a hearing of the Senate Committee on Environment and Public Works, Drinking Water, Fisheries and Wildlife Subcommittee, September 19, 1996 concerning S. 1660, the National Invasive Species Act of 1996:

Mr. Chairman and members of the Subcommittee, I am Dr. Eric Hallerman. I am an Associate Professor in Fisheries and Wildlife Sciences at Virginia Polytechnic Institute and State University. Currently, I am President of the Introduced Fish Section of the American Fisheries Society. While the broad mission of the Introduced Fish Section is to serve as an association of aquatics professionals interested in issues posed by introduced aquatic species, one of the objectives of the Section is to assist federal, state, and private groups in making informed decisions on introductions of aquatic species. Hence, I feel it is incumbent upon me to offer my perspective on S. 1660, reauthorizing the Non-Indigenous Aquatic Nuisance Prevention and Control Act of 1990 (P.L. 101-646). Because of the limited time from my learning of this hearing to the closing of the record of the hearing, I have not been able to have the Section vote approval of my comments. Hence, the testimony offered here is my own, though I am confident that my point of view is broadly shared among professional fisheries scientists.

Impacts of non-indigenous species. Introductions of non-indigenous aquatic species have led to negative ecological and economic impacts. One major mechanism for introductions has been discharge of ballast water from ships. Ballast water discharge has been blamed for the introductions of the zebra mussel, whose spread has caused hundreds of millions of dollars of control and damage costs for public and private institutions drawing water from affected ecosystems, significant declines of native mollusks, and reductions in recruitment of native fishes. Other less well-known introductions into the Great Lakes include spiny water flea, three-spined stickleback, round goby, and ruffe. These species negatively impact native species; for example, ruffe tends to displace yellow perch in affected areas of Lake Superior, and the round goby consumes lake trout eggs, impacting the recovery of this valued native species. Negative impacts associated with accidental introductions of non-indigenous aquatic species are not limited to the Great Lakes. Examples of unintentional introductions on other coasts include the Chinese mitten crab on the Pacific coast, the green crab on the Atlantic coast, and the brown mussel on the Gulf coast. Because the zebra mussel and other non-indigenous species continue to spread in watersheds throughout the country, their full negative ecological and economic impacts are not yet known.

Effectiveness of the Act. The focus of the Non-indigenous Aquatic Nuisance Prevention and Control Act of 1990 was to set up a framework for reducing the risk of unintentional introductions and to monitor and control non-indigenous aquatic nuisance species. The Act set up specific provisions for controlling zebra mussels and mandated that the Coast Guard promulgate regulations, that became effective in May 1993, to prevent further ballast water introductions into the Great Lakes. The Act authorized a research program, that among other accomplishments, identified materials that discouraged colonization of surfaces by zebra mussel larvae. It established an interagency Aquatic Nuisance Species Task Force to develop a framework to address the problem of non-indigenous aquatic nuisance species. Such interagency cooperation is essential for responding to problems that are not entirely in the authority provided to a single federal agency.

Actions mandated under the Act are widely considered among aquatics professionals to be positive developments. Reauthorization of the Non-Indigenous Aquatic Nuisance Prevention and Control Act is supported by resource managers on the front line of dealing with problems caused by non-indigenous aquatic species. The success of the approach as rather narrowly applied to zebra mussels and Great Lakes problems argues for its application to other non-indigenous species and to all American ports and associated waterways.

Recommendations. Against this background, I urge the Subcommittee to take two actions:

1. Report S. 1660 out of the Committee and lead an effective effort on the floor of the Senate to reauthorize the Non-Indigenous Aquatic Nuisance Prevention and Control Act of 1990. Because the Act has proven effective and requires only modest expenditures of public funds, its reauthorization should enjoy bipartisan support. I urge you to go forward with adoption of the bill. Some aquatic resources professionals argue correctly that impacts of non-indigenous species introductions are not limited to those within the scope of the bill. Clearly, not all non-indigenous species introductions are the result of ballast water discharges. For example, ecological and economic impacts have followed the deliberate stocking of favored, non-indigenous sport fishes in fresh waters. While these points are well taken from a biological standpoint, to include them within the scope of the bill under consideration would be a mistake politically. The success of the current aquatic nuisance species act implementation measures has rested in large part on consensus that these actions are justified on the basis of a well-defined and broadly recognized problem. Similar consensus is lacking on the wider range of problems posed by deliberate introductions of non-indigenous aquatic species, for example, on whether it is justifiable for federal actions to clash with state prerogatives on deliberate stocking of non-native trouts. Still other parties argue that problems posed by non-indigenous species are not restricted to aquatic ecosystems, and that introductions into terrestrial ecosystems also should be addressed by a bill of this nature. I feel that other public policies might be crafted to address other aspects of problems posed by non-indigenous species. To address the broadest range of introductions of non-indigenous species in the context of reauthorization of the Non-Indigenous Aquatic Nuisance Prevention and Control Act could lead to its defeat in this session of Congress.

2. Consider seriously the possibility of considering on the floor of the Senate the companion bill, H.R. 3217. The House Transportation Committee last week approved H.R. 3217, which justifiably goes further than S. 1660: (1) in authorizing funding for aquatic nuisance species research on the Atlantic, Pacific, and Gulf coasts, and (2) in establishing responsibilities for a Western task force on nuisance species. I feel that the thrust of the House bill, leading to a comprehensive national approach toward minimizing impacts of non-indigenous species introductions, is laudable. Though consideration of the House bill would involve suspension of the Senate rules, I do not anticipate objections from any quarter.

I am pleased to have had the opportunity to present my views, and thank you for consideration of my arguments.

Last Issue of ANS Digest?

While the future of the *Aquatic Nuisance Species Digest* is in question because of "fiscal realities in Washington D.C.", the editor, Nils Halker, has assembled another informative issue and is making plans for another year. The current issue contains articles on ... A National Forum on Aquatic and Marine Invasions, ... The Chesapeake Bay Basin, ... Preventing Nonindigenous Species Invasions in Prince William Sound, Alaska, A New Invader in the Kentucky River, The Round Goby: Innocent Until Proven Guilty?, and Biological Control of Purple Loosestrife--A New Control Method for a Tough Wetland Invader.

What can you do to get a copy and to help keep ANS Digest going? Contact Nils Halker, Editor, ANS Digest, Freshwater Foundation, Gray Freshwater Center, 2500 Shadywood Road, Navarre, MN 55331, USA. [e-mail: frshwtr@freshwater.org].

Aliens Listserver

.... Correspondent: Michael Morgan

Welcome to ALIENS-L - listserver of the Invasive Species Specialist Group (ISSG) of the IUCN Species Survival Commission. The group aims to "reduce the threats posed by invasive species to natural ecosystems and their native species, through increasing awareness of invasive species and means of controlling or eradicating them". This listserver is a contribution to that mission. It allows users to freely seek and share information on invasive species and the threats to the biodiversity of our planet. This listserver is not limited to members of ISSG but is available to all who might be interested in the invasive species subject.

The ISSG is a world wide network of experts on the conservation impacts of invasive species. Membership is by invitation, but it is not necessary to be a full member of the group to contribute to the cause of reducing conservation threats posed by invasive species. ISSG provides advice on threats from invasive species and control or eradication methods to IUCN members, conservation practitioners, and policy makers. The group concentrates on reducing or preventing the adverse effects of alien invasions on conservation values.

Because of the vast scope of the invasive species subject, ISSG activities are focussed on areas of special need. Sub-groups may develop to deal with areas such as terrestrial weeds, terrestrial vertebrates, invertebrates, fish, marine invasives, microorganisms, genetically modified organisms, and the international agreements and laws controlling invasive species. There is a special overall focus within the group on the particular threat which invasive species pose to oceanic islands.

This listserver is planned as an open forum to cover all of these invasive

Critical processess

species areas but it should not detract from other listservers which are established for a more specific purpose. The listserver manager will endeavour to maintain a list of other listservers and to share that with members of Aliens-L. This list of listservers can also be requested at any time. To subscribe, send a message to majordomo@ns.planet.gen.nz: skip the subject line and in the text area type: subscribe aliens-l

Pacific Introduced Species Symposium

.... Correspondent: Michael Morgan

A symposium on Marine/Aquatic Introduced Species in the Pacific will be held during the VIII Pacific Science Inter-Congress, July 13-19, 1997, Suva, Fiji. Papers on the ecology, biology, biogeography, environmental and human impacts, and management of introduced species are welcome, as are papers documenting new invasions, transport mechanisms, and intentional releases. The symposium is being co-sponsored by the CSIRO Centre for Research on Marine Pests (CRIMP) and the Pacific Science Association (PSA), and Ronald Thresher (CRIMP) and L. G. Eldredge (PSA) will Co-Chair the session; James T. Carlton will be the keynote speaker. The date will be announced later. For further information contact L. G. Eldredge [psa@bishop.bishop.hawaii.org] if you would like to present a contributed paper. Participants intending to present a paper are required to submit an abstract to the Inter-Congress Secretariat by January 31, 1997.

To obtain the Inter-Congress Second Circular which includes general program of the Inter-Congress, along with information on paper submission, accommodation, excursions, etc. contact: VIII Pacific Science Inter-Congress Secretariat c/o School of Pure & Applied Sciences, P.O. Box 1168, The University of the South Pacific, Suva, Fiji. FAX: (679) 314007. e-mail: psa@usp.ac.fj

Zebra Mussel CD-ROM Available from Army COE

A limited number of CDS covering zebra mussel biology and management are available from the Army Corps of Engineers. Contact: Dr. Michael J. Grodowitz, U. S. Army Corps of Engineers, Waterways Experiment Station, Attn: CEWES-ER-A, 3909 Halls Ferry Road, Vicksburg, MS 39180-6199, USA.

A Zoo of Intruders in San Francisco Bay

BERKELEY, Calif. (Aug 20, 1996 02:00 a.m. EDT; Copyright © 1996, New York Times Co. Reprinted by Permission) -- From the vantage point of the Berkeley Marina one recent morning, San Francisco stood sharply etched against a fog bank nestling along the Pacific shore like a gigantic roll of cotton candy, a recurring tableau essentially unchanged since Tony Bennett first left his heart in the city across the bay.

But ecologically speaking, the broad, aquamarine expanse of San Francisco Bay itself has been drastically reinvented.

Every 12 weeks on average, a new species of aquatic animal, plant or microbe from somewhere else in the world takes up residence in the bay. It has become what one expert, Dr. James T. Carlton of the Williams College Maritime Studies Program at Mystic, Conn., calls "an accidental zoo" -- a churning, chaotic cauldron of life in which scores of weird, wonderful creatures of ancient lineage that "never before met each other until just a moment ago in ecological time" have been thrown together. So far as is known, ecologists say, the bay is the estuary most invaded by exotic species in the world, and estuaries in general are the earth's most invaded marine ecosystems.

On that recent morning, Dr. Andrew N. Cohen, a marine biologist at the University of California at Berkeley who works closely with Carlton, directed a visitor's attention to an especially revealing gauge.

It was a block of orange Styrofoam, perhaps 3.5 feet by 1.5 feet, of the type that buoys the floating docks of Berkeley and other marinas. When lifted from the water, the block's underside appeared covered by a mass of multicolored moss and lettuce, black, brown, green, tan and yellow. But the plantlike organisms were actually colonies of marine animals, among them sponges and sea squirts, that cling to underwater surfaces around the bay in great masses. About a dozen species were visible, and invisible, uncounted microorganisms raised the total considerably.

"Virtually everything you see has arrived in San Francisco Bay from some other part of the world," Cohen said. That is the way it is the length and breadth of the bay's food web, from top predators like striped bass (introduced on purpose from the Atlantic Ocean more than a century ago) to microscopic protozoa from Japan.

Invasive species are seen almost everywhere in the world as human activity persistently rearranges the earth's flora and fauna. But San Francisco Bay offers a special window on where the global game of mix and match is leading at its most extreme. Species from other oceans now dominate the bay, and more are being crammed in all the time. They cover the bay's bottom virtually wall to wall, and no part of the larger bay ecosystem has escaped their impact; in some places they appear to account for all life.

They have, in fact, created a brand new ecosystem and perhaps, in time, will write a new chapter in evolution.

These exotic invaders (scientists have identified 212 such species so far, and the origins of 123 others are unknown) have arrived by a variety of avenues, from piggybacking on imported oysters to deliberate introduction to hitchhiking in boxes of fish bait. But the biggest single mechanism, scientists believe, is the ballast water from ships. Discharged routinely and daily into the bay in larger quantities from bigger vessels, ballast water is believed to have caused a marked acceleration of the invasion in the last decade.

Continuing invasions are changing the ecosystem so fast that scientists are doing well just to keep up with the growing inventory and distribution of species. Understanding the organisms' interactions and the characteristics of the new system has proved more elusive. Each new introduced species "can send it off in a different direction," Carlton said of the ecosystem, "and because I don't know what my next species is tomorrow, I don't know what to predict." Ecologists like Cohen and Carlton, the authors of an exhaustive study of the bay this year for the U.S. Fish and Wildlife Service, know that there are both positive and negative effects. For openers, there are many more species in the bay than before the invasions; the rich new ecosystem is in some measure a showcase of life's inventive variety.

But similar groupings of species are also being assembled in other estuaries around the globe while the bay's native flora and fauna dwindle in the face of the invasion from abroad. At least one bay species, the thicktail chub, has been driven to extinction. Another, the delta smelt, is endangered. A third, the Sacramento perch, can no longer be found in local waters. And many other native populations have been diminished. Invading predators may have contributed to the losses, Cohen said.

The bay has "lost the distinctive faunal characteristics and the web of community relationships that it had developed since its post-ice age origin, and which distinguished it from the other great estuaries of the world," the two ecologists wrote in a report last year.

While the worldwide conveyor belt has transferred at least a handful of San Francisco Bay species to distant estuaries, Cohen said, the extent and volume of the outbound transfer are not known. For terrestrial species, the flow is heavily from Europe and Asia to other parts of the world. For estuarine species, he said, "we don't have a handle on the preponderance one way or the other."

For good or ill, signs of the bay's transformation are everywhere.

"Oh, yes, all right!" Cohen exclaimed as he examined a tiny isopod, similar to the American pillbug that rolls up into a ball, that he had just extracted from a glob of biological material clinging to a dock at the Coast Guard station in Oakland. Cohen's excitement was the scientist's excitement over discovery, in this case directed at a recent arrival of Australian origin. But some of the isopod's relatives appear to be boring into and severely damaging the Styrofoam underpinnings of some docks, causing them to sink slowly.

At an arm of the bay within sight of the Oakland Coliseum, littleneck clams from Japan, exposed at low tide, cover the mud like smooth, gray stones. Some people harvest and eat them.

On Bay Farm Island, ribbed horse mussels, natives of the Atlantic, burrow into the mud between the low and high tide marks. They are in the bay by the millions, forming dense colonies. On Bay Farm Island, they bury themselves with just the tips of their double shells exposed and slightly separated. Scientists say they often clamp shut on the toes or bills of the endangered California clapper rail, sometimes causing adult birds to starve and chicks to drown. On the other hand, the mussels have become the rails' main food.

The rails' life is made further hazardous by two introduced land predators, the Norway rat and the red fox. Some measure of refuge from them has been provided by yet another aquatic invader -- Atlantic cordgrass, which thickly covers the shore of Bay Farm Island with a tall, thick protective blanket. But whether it is better habitat than the sparser Pacific cordgrass it is replacing is not known. Nor is it clear just how all of this ecological pulling and hauling will ultimately affect the endangered bird.

Farther south, on the bay shore near Hayward, Cohen reaches down with a long-handled net and brings up a haul of what look like black-eyed peas. They are tiny Asian clams, invaders that have covered large stretches of the bay's bottom at a peak density of more than 4,000 a square foot since their introduction a mere decade ago, probably as larvae in ballast water.

The clams are too small to have any economic value, but their effect on the life of the bay is enormous. They subsist on microscopic animals and plants, called zooplankton and phytoplankton, which form the basis of the bay's food chain. Scientists calculate that in the northern bay, where the clams are particularly dense, they can filter plankton from all the water in the deep channels more than once a day and all the water in the shallows, where phytoplankton especially abound, nearly 13 times a day. It is feared that the clams will permanently reduce the plankton, to the detriment of fish that feed in open water.

Another recent arrival from Asia, the Chinese mitten crab, so called because of its hairy claws, conjures fears of another sort. A native of Korea and China, it may have been planted in the bay as a food source. But its behavior when introduced outside its native range has sometimes been disturbing. In Germany in the 1930s, Cohen and Carlton wrote in their report, the invading crabs became "phenomenally abundant," with masses of them "migrating up the main rivers, piling up against dams, climbing spillways and swarming over the banks onto shore, sometimes wandering onto city streets and entering houses." No such onslaught has yet taken place here, but the crabs were first identified in the bay only two years ago.

An arrival in the late 1980s was the Atlantic green crab, a true aquatic Attila. "It eats virtually everything," Cohen said. A native of Europe, it made its North American landfall in New England, where in the 1950s it destroyed the soft-shell clam fishery. It may have been introduced here either in ballast water or, as in the case of some other species, as larvae in algae used to pack shipments of bait worms from New England. Here, the green crab has shown itself capable of eating the Dungeness crab, a valuable food species, and there is concern that it may eliminate the Dungeness from the bay. The green crab is too small to be a marketable replacement. In Bodega Harbor, green crabs can be collected by the score. There they eat the same shellfish that are eaten by native birds, and the concern is that the impact of the crab's depredations will cascade unpredictably through the food web.

Biological transformation has also overtaken the free-swimming creatures of the deep, open water. Gobies from Japan and shrimp from Korea, for instance, have joined the striped bass. In the fresher water of the delta at the northern end of the bay live species like goldfish, carp, threadfin shad and, from eastern North America, six species of catfish and four species each of sunfish and bass.

The economic effects of the introductions of new species have been little studied, but Cohen and Carlton say they are clearly substantial, though mixed. On one hand, according to their study, some introduced fish and shellfish have become valuable food and sportfishing species. Some, like mosquitofish, control nuisance insect populations. On the other hand, many of the exotics foul waterways and water delivery systems, damage docks, increase the cost of removing encrusting organisms from ships and prey on valuable native commercial and sport species.

Except in the Great Lakes, the Hudson River and Alaska, there are no government controls on the discharge of ballast water. Senator John Glenn, Democrat of Ohio, introduced a bill this year to extend regulations to all U.S. ports.

Even if all introductions stopped tomorrow, San Francisco Bay would hardly return to its former condition. While the settling-out of its new ecology is not yet complete, Cohen believes it might eventually fall into a pattern similar to that observed in terrestrial areas disturbed by humans. There, a relatively few hardy, adaptable, "weedy" species that thrive on disturbance tend to take over.

Stepping back and taking a philosophical look, Carlton predicted that whatever the character of the new ecosystem, it will in time come to be accepted as natural. No matter how great a creature's impact on the bay, he said, over the years it will gradually be seen as a normal part of the environment by people who do not realize it was an immigrant.

"Three or four generations into the future," he said, "it won't be an issue. Time heals all."

New St. Croix River Crossing Could Spread Zebra Mussels, Jeopardize Native Species

The U.S. Fish and Wildlife Service released a Biological Opinion to the Federal Highway Administration on August 30, which states that without precautions, construction of the bridge from Oak Park Heights, Minnesota, to St. Joseph, Wisconsin would jeopardize the existence of the endangered Higgins' eye pearly mussel and the winged mapleleaf mussel.

"We have worked closely with the states involved to enable their project to proceed while protecting the wildlife values and resources of the St. Croix River," said U.S. Fish and Wildlife Service Regional Director Bill Hartwig.

The Opinion was prepared as part of the consultation procedures that are required under the Federal Endangered Species Act to determine whether major construction by, or directed by, a Federal agency would adversely affect listed or proposed species.

The Service opinion further states that harm to the endangered mussels would be primarily due to construction barges inadvertently bringing zebra mussels into the St. Croix River. To allow the project to move forward while avoiding the likelihood of jeopardizing the existence of those species, the Minnesota Department of Transportation and the Federal Highway Administration agreed to require rigorous decontamination of construction barges to ensure that zebra mussels are not brought into the St. Croix River.

The Higgins' eye pearly mussel is found in the Mississippi River from Minnesota to southern Iowa. It is also in the Wisconsin and St. Croix Rivers. Unfortunately, all the waters that support Higgins' eye have been contaminated by zebra mussels, except for the St. Croix River. The winged mapleleaf mussel is even more critically endangered; it is found only in the St. Croix River.

Zebra mussel infestation can cause large-scale die-offs of native mussels. Zebra mussels have caused the elimination of native mussels in Lake Huron and portions of the Detroit River. No one yet knows the degree of impact that zebra mussels will have on native species in the Mississippi River, but large numbers of zebra mussels encrusted most of the native mussels that were pulled from the Mississippi River near Prairie du Chien, Wisconsin, during a recent mussel survey. Experts expect that zebra mussel infestation will cause, at a minimum, increased mortality at most of the mussel beds in the upper Mississippi River. Experts also predict that neither the Higgins' eye nor the winged mapleleaf would survive over time if the St. Croix River becomes contaminated with zebra mussels.

Nick Rowse, Service biologist for the project, said, The St. Croix River watershed is the premier mussel watershed of the Upper Mississippi River, and one of the premier mussel watersheds of the world. The river is considered a sanctuary containing the very best preserved pre-settlement (least human-impacted) aquatic community in the Upper Mississippi drainage. Prevention of zebra mussel contamination will not only protect the two endangered mussel species but will also protect the rich diversity of aquatic life that is found in the St. Croix River."

IFS Business Meeting Minutes, August 25, '96

1. Convene. Section President Neal Foster convened the meeting at the Hyatt Regency Hotel in Dearborn, Michigan at 3:30 PM.

2. Determination of quorum. Fourteen people were in attendance. However, only six were members of the Introduced Fish Section, and this was short of a quorum. Hence, no binding decisions could be made at the meeting.

3. Old business.

Treasurer's report. Neal Foster presented the Treasurer's report for Larry Zuckerman, who was unable to attend. The Section has 240 members, and their $4 annual dues are the Section's only source of income, $960 last year. Most of the Section's expenditures are printing and postage for the newsletter, $1936 last year. The shortfall was covered by drawing on our bank account, which now stands at $2553. Any IFS members wishing access to the detailed statement can contact current IFS officers.

Dues increase. Section dues, currently at $4, are the lowest of any Section in AFS. Given the shortfall in operating funds, a $1 rise in annual dues was approved unanimously by IFS officers in accordance with the Section by-laws. Since a disproportionate part of the costs for the newsletter are due to mailing costs to foreign IFS members, we will poll them in the next newsletter regarding their willingness to pay slightly higher annual dues.

Update on grass carp book. John Cassani asked the Section to provide $750, approximately half the project cost, toward producing 250 copies of the IFS-sponsored grass carp manual. In the absence of a quorum, no binding action could be taken. [Subsequent to the meeting, Bob Kendall of the AFS publications office suggested that the Section apply for use of interest on the publications program endowment to support this project. John Cassani and incoming President Eric Hallerman will pursue this means of funding.]

Past-President's plaque. Incoming President Eric Hallerman presented outgoing President Neal Foster with his Past-President's plaque, and thanked him for his term of service.

4. New business.

Encourage attendance of Section symposia. Eric Hallerman encouraged all present to attend the three Section-sponsored or co-sponsored symposia: (1) Introductions of non-indigenous fishes and other aquatic species, (2) Assessing and managing risks posed by genetically modified aquatic organisms, and (3) Private aquaculture safeguards for Great Lakes biological integrity.

Nominations for section offices. Two Section offices were open. Nominations will be sought for President-Elect, and ballots distributed in the next Section Newsletter [see related item]. John Cassani agreed to serve as Newsletter Editor, and will be assisted by outgoing editor Don Baltz through the transitional period.

Organize IFS symposium for next year's AFS meeting. Topics were sought for a Section-sponsored symposium for next year's AFS annual meeting in Monterrey, California. Ex-President Denny Lassuy had submitted a written proposal for a symposium exploring the role of public and private aquariums. Discussion at the meeting was favorable, and suggestions included keeping the tone of the symposium balanced and inviting participation of organizations such as the Native Fishes Society. Consensus on encouraging Denny to go forward does not preclude proposal of other Section-sponsored symposia.

Electronic communications. Eric Hallerman led discussion of various options regarding enhancing Section function by use of electronic communications. Consensus was reached: (1) that access to a listserver to be set up will not, at least at first, be restricted to Section members, and (2) that the listserver will supplement, but not replace, the newsletter. Support was noted for creation of a World Wide Web homepage for IFS. Suggestions were taken on where to support it and on possible hot links to other websites.

Possible Section activities in the policy arena. Noting that AFS can favorably influence public policy formulation, Eric Hallerman suggested the possibility of the Section expressing support for renewal and broadening of the Non-indigenous Aquatic Nuisance Species Act of 1990. Support was noted for working toward this end [see related stories].

New business from the floor.

Awards program. The AFS Professionalism Committee has developed a model awards program, and suggests that each subunit consider establishing or expanding the number of its awards. Discussion revealed interest in the possibility of establishing awards for students, for professionally-established IFS members, and for individuals outside of AFS. [see related item in this Newsletter.]

Skinner Fund. Interest on the Skinner Memorial Fund is awarded by the Education Section to worthy students to support their attendance at the AFS annual meeting. Interest rates being low, few awards of limited size would be made this year, but for a $3000 donation by the Education Section. Education Section President (and Past IFS President) Chris Kohler asked the IFS to consider making a donation. Discussion led to consensus that a token $100 donation be made subject to approval by the membership through a check-off in the next Newsletter [see related item]. IFS members also are encouraged to make individual donations to the Skinner Fund.

AFS 2000. The Fisheries Administrators Section has challenged all other sections to donate $1000 to the AFS 2000 campaign. Discussion led to consensus that IFS simply cannot respond to the challenge.

5. Adjourn. We adjourned at 5:00.

Minutes respectfully submitted,
/s/Eric Hallerman

Fisheries News

.... Correspondent: Gene Buck

[Gene is Senior Analyst for the Congressional Research Service and publishes weekly summaries of fish related issues for Congress. This selected subset of items of potential IFS interest was extracted from <FISH -ECOLOGY@SEARN.SUNSET.SE> with Gene's permission. Gene is always looking for new fisheries issues to communicate to Members of Congress and their staff. Editor]

Items in this summary were excerpted from a variety of news and information sources. CRS is not responsible for the accuracy of the various news items. I [Gene] would appreciate your feedback on this summary. Comments should be directed gbuck@crs.loc.gov.

To further assist me [Gene] in providing a broad scope of information resources to Congress, I would appreciate being added to any mailing lists of publications, news releases, newsletters, etc. relevant to marine mammals and fisheries. Where there is a subscription cost, a sample copy would provide a basis for deciding whether or not a subscription could be justified. Archived summaries from the first Friday of each month since July 1994 are available at "http://www.lsu.edu/~sglegal/summaries.html". --Gene Buck, CRS-ENR, Library of Congress, Washington, DC 20540-7450;

Taura Syndrome Virus. On Sept. 5, 1996, TX Parks and Wildlife Dept. officials and shrimp farmers announced that the Taura syndrome virus was detected in August 1996 at six coastal shrimp hatcheries from the Rio Grande Valley north to Matagorda Bay, although this outbreak appears not to be as widespread nor as virulent as last year's. Shrimp farmers have been asked to harvest infected shrimp and hold pond water for at least 10 days before discharge to minimize any potential threat to wild shrimp. [Assoc Press]

Tilapia Pathogen. The Aug. 23, 1996 issue of Science reported that a bacterium, Streptococcus iniae, causing human meningitis has been transmitted from Tilapia to humans. Transmission was believed to be through injuries received while cleaning fish. Six individuals in Ontario were affected -- one with meningitis and transient arthritis and the other five with skin or blood infections. [Science]

Diseased Fish Destroyed. On Aug. 19, 1996, Michigan Dept. of Natural Resources officials announced that 245,000 Kamloops rainbow trout, obtained from a Montana hatchery as eggs, would be destroyed after learning that federal officials had detected parasites in fish at the Montana hatchery that were not present in the Great Lakes basin. [Assoc Press]

Bring Back the Natives. On Aug. 20, 1996, the National Fish and Wildlife Foundation, in cooperation with the U.S. Forest Service, Bureau of Land Management, Bureau of Reclamation, and Trout Unlimited, announced 26 projects nationwide to restore native fish species on public lands by restoring watersheds as part of the "Bring Back the Natives" program. [Assoc Press]

Canadian Sea Lamprey Funding Restored. On Aug. 7, 1996, Canada's Minister of Fisheries Fred Mifflin announced that Canada will provide C$5.145 million for the Great Lakes Sea Lamprey Control Program for the 1996-97 and 1997-98 fiscal years. This Program is conducted by the U.S.-Canada Great Lakes Fishery Commission. [Canadian govt. press release]

Tui Chub in Diamond Lake. On Sept. 20-21, 1996, the Oregon Fish and Wildlife Commission will meet to consider alternatives for eradicating introduced tui chub in Diamond Lake. Costs may exceed $1 million if rotenone is used and an environmental impact statement is required. [Assoc Press]

Invasive Species. On Oct. 22, 1996, the Nature Conservancy released a report "America's Least Wanted" calling attention to concerns for non-native species introductions. The report suggests these introductions have cost the U.S. economy billions of dollars and have contributed to the decline of 42% of U.S. threatened and endangered species. [The Nature Conservancy press release via Greenwire, Congr. Record]

Farmed Salmon Problems. On Oct. 24, 1996, the David Suzuki Foundation released a report claiming the farmed salmon industry is jeopardizing British Columbia's wild salmon stocks and posing risks to human health through unregulated drug use. The report recommends that open-ocean rearing be replaced with contained systems prohibiting contact with the ocean, that drug use be much more closely monitored, that the spread of drug-resistant diseases be monitored, that only native salmon be reared, that the industry be required to carry insurance covering full ecological restoration of catastrophic events, and that sewage from salmon farms not be discharged into the ocean. [Assoc Press, David Suzuki Foundation press release]

President-Elect Candidates

Charles L. Brown received his B.S. in 1972 from St. Norbert College and M.S. in 1974 from the University of Arkansas. Currently, he is an ecologist at the Washington DC headquarters of the U. S. Department of Agriculture's, Animal and Plant Health Inspection Service (APHIS), which is the main federal agency involved in prevention and control of nuisance organisms. While with APHIS, Charlie has been involved with assessing the environmental risks associated with field testing of genetically modified organisms, and he has actively pursued issues involving aquaculture and aquatic nuisance species. Prior to joining APHIS, he spent 13 years with the U.S. Fish and Wildlife Service conducting fish habitat research at the Great Lakes Science Center in Ann Arbor, Michigan. Charlie has twice received the James W. Moffett Award, which recognizes the best scientific publication of the Center.

Now is an exciting time for the Introduced Fish Section. Policies and laws regarding introduced fishes and other aquatic organisms are rapidly being made, and it is essential that decision makers be aware of the best available scientific information. Because the issues regarding introduced organisms are often complex, it is neither likely, nor is it essential, that our Section's members always speak unanimously. Charlie's goal as President would be to develop the awareness - among Section members as well as decision makers - of the scientific evidence regarding the effects introduced aquatic organisms can have on existing ecosystems.

Anna Toline is a conservation geneticist in the Department of Fisheries and Wildlife at Utah State University. Her research focuses on the application of population genetics to recovery and management of native aquatic species (particularly fish). To this end, her research focus can be partitioned into three general categories: 1) effects of hybridization of native species with introduced species, 2) assessment of among-population genetic structure (of native species) for identification of management units, and 3) quantification of genetic variability within populations and assessment of genetic differences among individuals used as broodstock for recovery.

Much of her interest in introduced fish stems from having the opportunity to participate in native species recovery programs in the state of Utah. Introduction of non-native species has been identified as a serious threat to several native species and her role includes the application of genetics to aid in recovery. One particular project includes the development of methods to distinguish between cutthroat and rainbow trout. She is using genetic markers in conjunction with data from other researchers and the state agency to identify hybrids to 1) understand the influence of introduced rainbow trout on native cutthroat trout, 2) identify pure species of cutthroat trout for recovery, and 3) identify genetically distinct stocks as potential sources for broodstock for augmentation and reintroduction.

Anna has been a member of AFS for ten years and has been involved in the Genetics Section, the Introduced Fish Section, the Endangered Species Technical Committee of the Western Division and is on the Program Committee for the 1997 AFS Annual Meeting in Monterey. Her goal within the Introduced Fish Section is to heighten awareness of the effects of introduced species on native species. She would like to examine ways in which we can use our various backgrounds to improve the status of our native species. She is looking for feedback as to how this can best be approached and would welcome input from all sources.

IFS Ballot

Vote for one President-elect candidate:

__ **Charles L. Brown**

__ **Anna Toline**

Vote yes or no to:

__ Support IFS donation of $100 to Skinner Memorial Fund.

For international members only, vote yes or no to:

__ Raise your section dues by US$2.

Ballot deadline is **December 15, 1996.**

Mail Ballot to Eric Hallerman, Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061-0321

1996-1997 Officers

President: Eric Hallerman, Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061-0321; (540) 231-5573; FAX 231-7580; e-mail: ehallerm@vt.edu

President Elect: Open, pending outcome of election.

Secretary-Treasurer: Larry Zuckerman, Kansas Department of Wildlife and Parks, 512 S.E. 25th Ave., Pratt, KS 67124-8174; (316) 672-5911

Past President: Neal R. Foster, U.S. Dept. of Interior, Nat'l Biological Service, Great Lakes Science Center, 1451 Green Road, Ann Arbor, Michigan 48105-2807; Phone[+voicemail](313) 994-3331-x264; FAX: 994-8780; e-mail: nealfost@umich.edu or neal_foster@nbs.gov

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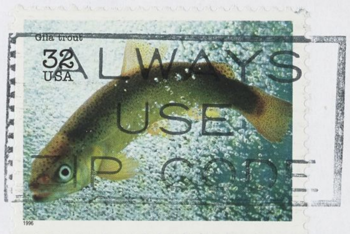

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Articles

How Many Species Are There on Earth?

ROBERT M. MAY

This article surveys current answers to the factual question posed in the title and reviews the kinds of information that are needed to make these answers more precise. Various factors affecting diversity are also reviewed. These include the structure of food webs, the relative abundance of species, the number of species and of individuals in different categories of body size, along with other determinants of the commonness and rarity of organisms.

Over a century ago, Darwin and others provided the broad outline of an answer to the question of how life has evolved on Earth and how species originate. The next question would seem to be how we use this basic understanding to estimate—from first principles—how many species are likely to be found in a given region or, indeed, on Earth as a whole.

Surprisingly, this question of "how many species?" has received relatively little systematic attention, from Darwin's time to our own. At the purely factual level, we do not know to within an order of magnitude how many species of plants and animals we share the globe with: fewer than 2 million are currently classified, and estimates of the total number range from under 5 million to more than 50 million. At the theoretical level, things are even worse: we cannot explain from first principles why the global total is of the general order of 10^7 rather than 10^4 or 10^{10}.

This article first surveys various kinds of empirical and theoretical studies that are helping to give us a better idea of how many species, or how many individual organisms, we might expect to find in a given environment. Such studies include the structure of food webs, patterns in the relative abundance of species, patterns in the number of species or number of individuals in different categories of physical size, and general observations about trends in the commonness or rarity of organisms. The article then reviews current evidence about the total number of species on Earth, indicating lines of research that could sharpen the estimates. We do not end up with a list of answers, but rather with a list of more sharply focused questions.

The Structure of Food Webs

Cohen and Briand (*1, 2*) have compiled and analyzed a catalog that now includes 113 food webs, embracing a wide variety of natural environments (55 food webs from continental settings—23 terrestrial and 32 aquatic—along with 45 coastal and 13 oceanic webs). The data for these food webs are of uneven quality, with the most notable problem being that some studies identify individual species ("blue jays") whereas others deal with aggregates ("spiders," "copepods," or even "zooplankton"); some studies articulate individual species of predators at upper levels but aggregate coarsely at lower trophic levels (*3*). Even so, some remarkable regularities emerge from Cohen and Briand's analysis of these data (*1, 2*).

For one thing, the average number of other species with which any one species interacts directly is consistently around 3 to 5 (*4*). The number is consistently higher (average, 4.6) in relatively constant environments than in fluctuating ones (average, 3.2). There are also consistent and quantitative patterns in the proportions of basal, intermediate, and top predator species (those whose links reach only upward, both ways, and only downward, respectively); the ratios are 0.19 : 0.53 : 0.29, respectively (*5*). A similar pattern of "link-scaling" invariance is found for the ratio of links among the four categories of basal-intermediate, basal-top, intermediate-intermediate, and intermediate-top (0.27 : 0.08 : 0.30 : 0.35, respectively). Most interestingly, these two quantitative patterns in the proportions of species in different trophic categories, and in "link-scaling," can be deduced from the empirical observation that each species is directly connected to roughly four others, along with

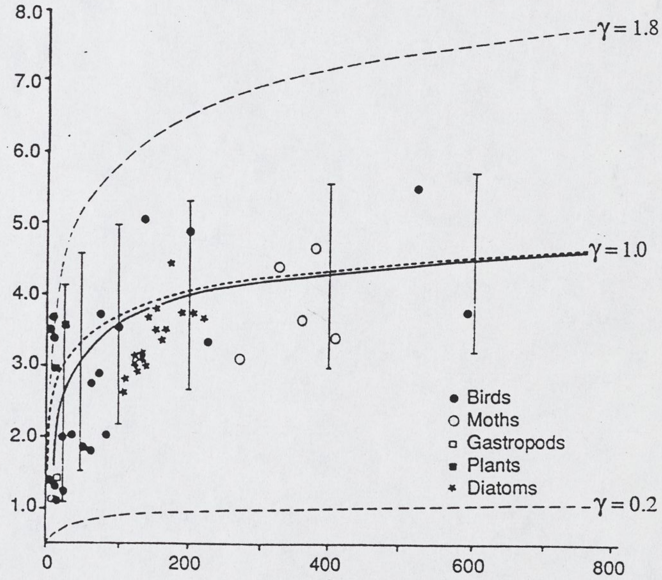

Fig. 1. A plot of S, the number of species, versus σ, the standard deviation of the logarithms of the relative abundances, for various communities of birds, moths, gastropods, plants, and diatoms. The dashed line labeled $\gamma = 1.0$ shows the relation between S and σ for Preston's (*15*) "canonical" lognormal distribution; the lines labeled $\gamma = 0.2$ and $\gamma = 1.8$ are the bounds to the range of S-σ relations that might be expected from general mathematical properties of the lognormal distribution, for large S and reasonable ranges of values for the total number of individuals, N. The solid line is the mean relation predicted by Sugihara's (*17*) model, and the error bars represent ±2 standard deviations about this mean.

This article was written while the author was in the Department of Biology, Princeton University, Princeton, NJ 08544. His present address is Department of Zoology, Oxford University, Oxford, OX1 3PS, England.

Table 1. The distribution of 160 plant species from the *Biological Flora of the British Isles*, classified into eight categories according to geographic distribution (wide or narrow), habitat specificity (broad or restricted), and local abundance (somewhere large or everywhere small) (*34*).

Local population size	Geographic distribution			
	Wide habitat specificity		Narrow habitat specificity	
	Broad	Restricted	Broad	Restricted
Somewhere large	58	71	6	14
Everywhere small	2	6	0	3

the assumption that the species are ordered in a cascade or hierarchy, such that a given species can prey on only those below it and can be preyed on only by those species above it in the hierarchy [an assumption that several authors (*2, 6*) have independently suggested may follow from body-size considerations between predators and their prey].

Other patterns in the ratios between numbers of interacting species in different trophic levels are the subject of continuing investigation. Hawkins and Lawton (*7*) have observed that food chains comprising green plants, insect herbivores, and insect parasitoids include over half of all known species of metazoans, so that understanding what determines the richness of parasitoid species could be a major step toward understanding the diversity of terrestrial communities. They analyzed data for 285 species of herbivorous insects, from 42 families, in Britain, and found the typical such species to be attacked by 5 to 10 species of parasitoids; the number depends significantly on the geographical range of the host insect, on the architecture of the host plant, and to a lesser extent on a variety of other factors (*7*). Preliminary data suggest that the tropics are roughly similar to Britain, in that herbivorous insects are hosts to around five to ten species of parasitoids (*8*). Other studies document systematic patterns in the number of phytophagous insect species associated with different plant hosts (*9*) and in the ratios between numbers of species of prey and predators of various kinds (*10*).

It could be that many of these apparent patterns tell us more about the workings of the human mind, and about how we tend to collect and categorize data, than they do about the natural world (*11*). Moreover, the populations in real food webs can have extremely complex dynamical behavior, with nonlinearities in density-dependent factors producing cyclic or chaotic changes in abundance and with unpredictable environmental fluctuations adding further complications; it seems unlikely that the salient features of such dynamical systems can be captured in static analyses of food web graphs (*12*). These caveats and complications notwithstanding, the patterns discussed above are intriguing. If they stand up to further study, they could simplify the task of understanding diversity. It could be, for example, that one need only understand what determines the number of plant species, and then the total faunal diversity could be deduced from appropriate rules.

Relative Abundance of Species

Real understanding of food webs in particular, and of diversity in general, must go beyond the mere presence or absence of species to an understanding of relative abundance. In early successional communities, and in environments disturbed by toxins or "enriched" by pollution, steeply graded distributions of species relative abundance (SRA) are commonly seen, with a handful of dominant species accounting for most of the individuals present. Conversely, in relatively undisturbed "climax" communities consisting of many species, relatively even distributions of relative abundance are typical; very often, such SRAs are distributed according to a "canonical lognormal" distribution, as illustrated in Fig. 1. Such trends in SRAs show up in studies of old field succession (*13*). The effects of pollution or other systematic disturbances reveal the same trend, except that time effectively runs backward, so that the progression is from evenness to dominance (*14*).

It is not surprising that the relative abundances within a fairly large and relatively undisturbed group of species will be disturbed lognormally. The relative abundances are likely to be governed by the interplay of many more or less independent factors. It is in the nature of the equations of population dynamics that these several factors should compound multiplicatively, and the statistical central limit theorem applied to such a product of factors implies a lognormal distribution. This general observation, however, tells us nothing about the relation between σ (the standard deviation of the logarithms of the relative abundances) and S (the total number of species present). The puzzling fact is that very many assemblies have SRAs that obey the canonical lognormal distribution, that is, that have the unique relation between σ and S illustrated by the curve labeled $\gamma = 1.0$ in Fig. 1, although this curve represents just one of an infinite family of possible lognormal distributions (*15*).

It has been conjectured that the canonical property may be merely an approximate mathematical property of all lognormal distributions for large S; the dashed curves in Fig. 1 labeled $\gamma = 1.8$ and $\gamma = 0.2$ represent plausible boundaries to the σ-S relation on this basis (*16*). The data put together by Sugihara (*17*) in Fig. 1 make it clear, however, that real SRAs obey the canonical relation more closely than can be explained by these mathematical generalities alone. Sugihara has also suggested a biological mechanism that will produce the observed patterns. He imagines the multidimensional "niche space" of the community as being a hypervolume broken up sequentially by the component species (with any fragment being equally likely to be chosen for the next breakage, regardless of size), such that each of the S fragments denotes the relative abundance of a species. Although the biological status of this assumption is debatable, it generates patterns of SRA in accord with a large number of data (the solid line in Fig. 1 shows the mean relation between S and

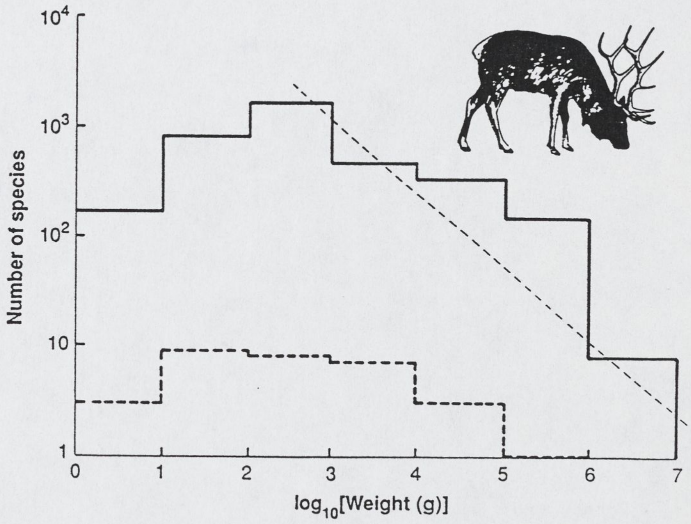

Fig. 2. The numbers of species, S, of all terrestrial mammals (solid histogram) and of British mammals (dashed histogram), excluding bats, are shown distributed according to mass categories (mass expressed in grams) (*18, 19*). Note the doubly logarithmic scale. The thin dashed line illustrates the shape of the relation $S \sim L^{-2}$, where L is the characteristic length (*20*).

σ predicted by the model, and the error bars show the range of ±2 standard deviations about the mean). Such a fit does not, of course, validate the model; it is possible that other biological assumptions could produce similar distributions of SRA.

One problem with essentially all the data that have been compiled for SRA is that they focus on particular taxonomic groups ("birds," "moths"). To understand how communities are assembled, it may be more relevant to inquire about the relative abundance within ecologically similar groups (putting birds together with bats and some large insects, for instance).

Number of Species Versus Physical Size

A variety of other patterns in the distribution and abundance of organisms have received little attention. For example, how many species do we expect to find in different categories of physical size, within a given region?

The meager amount of available information bearing on this question is reviewed elsewhere (*18*). Figure 2 gives one representative study, showing the way in which all 3000 or so mammalian species, excluding bats and marine mammals, are apportioned among mass classes (*19*). A corresponding analysis, but restricted to the mammal species of Britain, again excluding bats and marine mammals, is also shown in Fig. 2 (*18*). Although Britain's mammals appear to obey the global pattern of species versus size, appropriately scaled down, this may not be true in general; there is no a priori reason to expect the species-size patterns for faunal assemblies from relatively small areas to be the same as those from large (and correspondingly more environmentally diverse) areas.

Figure 2 and similar analyses represent rough assessments of the facts. Very few ideas have been advanced in explanation of these facts about species-size distributions. Hutchinson and MacArthur (*20*) have advanced arguments for expecting an L^{-2} relation between the number of species and the characteristic length of constituent individuals, L. The argument is essentially that, for terrestrial organisms, the world is seen as two-dimensional, and therefore the possibility of finding new roles (and thence new species) may scale as L^{-2}. This conjectured L^{-2}, or $M^{-2/3}$, relation, where M is mass, is illustrated by the dashed straight line in Fig. 2.

Number of Individuals Versus Physical Size

Other patterns can be sought in the relation between numbers of individuals and their physical size (mass or characteristic length). For example, in a particular region, how is the number of individual animals in the size class from 0.1 to 1 cm related to the number in the class from 1 to 10 cm (*21, 22*)?

In particular, Morse *et al.* (*21*) and Brown and Maurer (*23*) have collated data about populations of phytophagous insects and of birds, respectively, and have advanced qualitative explanations for these data. Morse *et al.* began with the assumption that roughly equal amounts of energy flow through each size category; although very unlikely to be true in general, this assumption is supported by some evidence from organisms ranging widely in size (*24*). Given this assumption, along with the usual manner in which metabolic costs become relatively larger at smaller sizes, the total number of individuals, N, in the size class with characteristic mass M and length L may be expected to scale as $N \sim M^{-0.75} \sim L^{-2.25}$ (*25*). That is, for a 10-fold decrease in characteristic length we would, on this basis, expect a roughly 180-fold increase in the total number of individuals.

Recent insights into the fractal geometry of nature suggest, however, that the structure of the habitat—and hence the number of possible ways of making a living—is unlikely to scale linearly with L (*26*). Consider, for example, the circumference of a large tree, or any other "one-dimensional" object. If we measure it on a 10-cm scale, we get one answer. On a 1-cm scale, we will often get another, larger answer. A yet larger answer would be obtained on a 1-mm scale, and so on. The circumference of the tree is thus not simply one dimensional but has a "fractal dimension," D, such that the perceived length, $\ell(\lambda)$, depends on the step-length of measurement, λ, as λ^{1-D}: $\ell(\lambda) = c\lambda^{1-D}$, where c is a constant. If $D = 1.5$, for example, a 10-fold reduction in the measurement scale (from, say 10 cm to 1 cm) will result in the apparent length increasing by a factor $10^{0.5} \simeq 3$. Morse *et al.* applied these notions to measure the profiles of various kinds of vegetation at different scales, concluding that D for such habitats ranged from around 1.3 to around 1.8, with an average around 1.5 (Fig. 3). That is, for herbivorous insects that exploit their surroundings in an essentially one-dimensional way (using the edges of leaves, or the like) a 10-fold decrease in physical size produces a roughly 3-fold increase in the apparently available

Table 2. The number of species (to within an order of magnitude) in the different animal phyla, classified according to the habitat of adult animals. Most phyla are predominantly marine and benthic, some exclusively so. The numbers 1 through 5 indicate the approximate number of recorded living species: 1 means 1 to 10^2; 2 means 10^2 to 10^3; 3 means 10^3 to 10^4; 4 means 10^4 to 10^5; and 5 means 10^5 or more. After (*38*). Abbreviations: B, benthic; P, pelagic; M, moist; X, xeric; Ec, ecto; and En, endo.

Phylum Subphylum	Habitat							
	Marine		Freshwater		Terrestrial		Symbiotic	
	B	P	B	P	M	X	Ec	En
Porifera	3		1				1	
Placozoa	1							
Orthonectida								1
Dicyemida								1
Cnidaria	3	2	1	1			1	
Ctenophora	1	1						
Platyhelminthes	3	1	3		2		1	4
Gnathostomulida	2							
Nemertea	2	1	1		1		1	
Nematoda	3	1	3	1	3	1	3	3
Nematomorpha								2
Acanthocephala								2
Rotifera	1	1	2	2	1		1	1
Gastrotricha	2		2					
Kinorhyncha	2							
Loricifera	1							
Tardigrada	1		2		1			
Priapula	1							
Mollusca	5	1	3		3	1	1	1
Kamptozoa	1		1				1	
Pogonophora	2							
Sipuncula	2				1			
Echiura	2							
Annelida	4	1	2		3		2	
Onychophora					1			
Arthropoda								
Crustacea	4	3	3	2	2		2	2
Chelicerata	2	1	2	2	4	3	2	1
Uniramia	1	1	3	2	5	3	2	2
Chaetognatha	1	1						
Phoronida	1							
Brachiopoda	2							
Bryozoa	3		1					
Echinodermata	3	1						
Hemichordata	1							
Chordata								
Urochordata	3	1						
Cephalochordata	1							
Vertebrata	3	3	2	3	3	3	1	1

habitat; for creatures that exploit their environment in an essentially two-dimensional way (using surfaces rather than edges), the effect must be squared, so that a 10-fold decrease in physical size produces an effectively 10-fold increase in apparent habitat. These two factors (the one-dimensional factor 3 and the two-dimensional factor 10) are likely to bound the range of possibilities found in actual assemblies of insects.

Combining these fractal aspects of habitat perception with the metabolic considerations discussed above, Morse *et al.* concluded that a 10-fold decrease in characteristic length, L, is likely to produce an increase in N that lies between 500 and 2000 (that is, roughly between 3 and 10 times 180). As shown in Fig. 4, this very rough expectation is borne out surprisingly well by data for the number of individual arthropods of different body lengths found on vegetation in places ranging from primary forests, primary riparian vegetation, and secondary vegetation in the New World Tropics to temperate habits, for example, birch trees on Skipwith Common in Yorkshire.

The study by Morse *et al.* is a frankly speculative one. I have chosen to highlight it because it provides an explicit example where our thinking about aspects of population abundance and diversity needs to acknowledge that nature is often not Euclidean but rather may have fractal geometry, with organisms existing in spatial and temporal frameworks that are, as it were, jagged on every scale (*27*). This is an example where new mathematical concepts interact with biological ideas in potentially surprising ways (the chaotic behavior of many simple population models is another example).

Species Numbers, Species Abundance, and Body Length

Still other studies have focused on empirical relations between the abundance of individual species and the body size of constituent individuals (*25, 28*). I think any eventual understanding of the total number of species in a given environment, and thence ultimately of the diversity of life on Earth, will need to be based on a clear understanding of the interplay among all the factors discussed above. Yet most of the few existing studies have singled out one or other aspect (species size, species abundance) from the interwoven mosaic.

Exceptions are the work on birds by Brown and Maurer (*23*) and the recent study by Morse *et al.* of the relations among species number, species abundance, and body length for 859 species of arboreal beetles in lowland rain-forest trees in Borneo (*29*). Figure 5A summarizes the results, showing the total number of species in different categories of population abundance and physical size (both plotted logarithmically); Fig. 5, B through E, correspondingly shows the number of species in different trophic categories. Although Fig. 5 does have some interesting structural details [for discussion, see (*29*)], it is essentially simple. It is encouraging that Fig. 5 has the basic features one would have guessed from the separate studies of species abundance, species size, and abundance size in different groups, as discussed above.

Commonness and Rarity

In the discussion above, some of the species found in a given region are confined to that region, whereas others (which are part of the species-size and other distributions in the region) are distributed much more widely. Partly for this reason, and partly for its intrinsic interest, it would be nice to know more about the distribution of geographical ranges within different taxonomic groups of species. What fraction of all bird species, for example, range globally over 10% of the globe, over 1%, and so on? Hanski (*30*), Brown (*31*), Root (*32*), Rapoport (*33*), and others have made a start toward answering this question, for diverse collections of organisms including vascular plants, intertidal invertebrates, terrestrial arthropods, planktonic crustaceans, and terrestrial vertebrates (especially birds), but much remains to be learned.

Intuitive ideas about commonness and rarity usually make reference both to geographical distribution and to local abundance. Such considerations often swirl together in ways that make it difficult to define exactly what constitutes a rare species. One type of rareness is, for example, exhibited by the silver sword, *Argyroxyphium macrocephalum*, that grows only in the crater of the Haleakala volcano on Maui. Although there are around 50,000 individuals in the large,

Table 3. A rough indication of the relative effort devoted to animals from different taxonomic groups is given by the average number of papers listed in the *Zoological Record*, 1978 through 1987 (*54*).

Phylum / Subphylum / Class / Order	Average number of publications per year (coefficient of variation, in percent)	Approximate number of recorded species	Papers per species per year
Protozoa	3,900 (10)	260,000	0.15
Porifera	190 (22)	10,000	0.02
Coelenterata	740 (12)	10,000	0.07
Echinoderma	710 (15)	6,000	0.12
Nematoda	1,900 (1)	1,000,000 (?)	0.002
Annelida	840 (9)	15,000	0.06
Brachiopoda	220 (14)	350	0.63
Bryozoa	160 (15)	4,000	0.04
Entoproctra	7 (53)	150	0.04
Mollusca	1,000 (8)	100,000	0.04
Arthropoda			
Crustacea	3,300 (9)	39,000	0.09
Chelicerata			
Arachnida	2,000 (6)	63,000	0.03
Uniramia			
Insecta	17,000 (7)	1,000,000 (?)	0.02
Coleoptera	2,900 (6)	300,000	0.01
Diptera	3,200 (7)	85,000	0.04
Lepidoptera	3,500 (9)	110,000	0.03
Hymenoptera	2,200 (9)	110,000	0.02
Hemiptera	1,700 (7)	40,000	0.04
Chordata			
Vertebrata			
Pisces	7,000 (13)	19,000	0.37
Amphibia	1,300 (12)	2,800	0.47
Reptilia	2,400 (7)	6,000	0.41
Aves	9,000 (10)	9,000	1.00
Mammalia	8,100 (12)	4,500	1.80
	Mammalian orders		
Monotremata	20	3	6.8
Marsupialia	269	266	1.0
Insectivora	270	345	0.8
Dermoptera	2.2	2	1.1
Chiroptera	402	951	0.4
Primates	956	181	5.3
Edentata	38	29	1.3
Pholidota	5	7	0.7
Lagomorpha	173	58	3.0
Rodentia	1,538	1,702	0.9
Cetacea	360	76	4.8
Carnivora	1,157	231	5.0
Tubulidentata	2.7	1	2.7
Proboscidea	94	2	47
Hyracoidea	12	11	1.0
Sirenia	43	4	10.8
Perissodactyla	142	16	8.9
Artiodactyla	1,124	187	6.0
Pinnipedia	218	33	6.6

·local population of this plant, its restriction to the one volcanic crater would make it very rare by most definitions. Another type of rareness is exhibited by the grass *Setaria geniculata*, which is found from Massachusetts to California and on down through tropical South America to Argentina and Chile but which is not abundant anywhere. This grass is rare in the sense that its populations are "chronically sparse" (*34*) everywhere in its broad range.

There have been a variety of proposals for codifying ideas about commonness and rarity. In particular, Rabinowitz *et al.* (*34*) have considered three different kinds of questions that arise in thinking about rarity: (i) is the species distributed over a broad geographical area, or is it endemic to some restricted location; (ii) whatever its range, is the species found in a wide variety of habitats, or is it specialized to one kind of site; and (iii) is the species abundant somewhere in its range, or are its numbers everywhere small. These three considerations combine to give eight categories, only one of which (broad distribution, unspecialized habitat, large populations) ordinarily corresponds to the species being called "common." Rabinowitz *et al.* noted that the archetypal "rare" species, with narrow distribution, specialized habitat, and small numbers, represents only one of several different kinds of rarity. These investigators pursued their ideas by applying them to the plants surveyed in the *Biological Flora of the British Isles* (which gives detailed distribution maps and notes about the habitat and population of 177 of the 1822 native British plants). Rabinowitz *et al.* asked 15 colleagues to classify each of the 177 species according to the eightfold category scheme described above (*35*). This process gave clear consensus for 160 of the 177 species, and the results are summarized in Table 1.

Most species (149 versus 11) are abundant somewhere, and most species (137 versus 23) have a wide geographical range (Table 1). A narrower majority (94 versus 66) have restricted habitat specificity.

Of the eight categories, species with wide ranges and large population sizes, but restricted habitat specificities, predominate (71

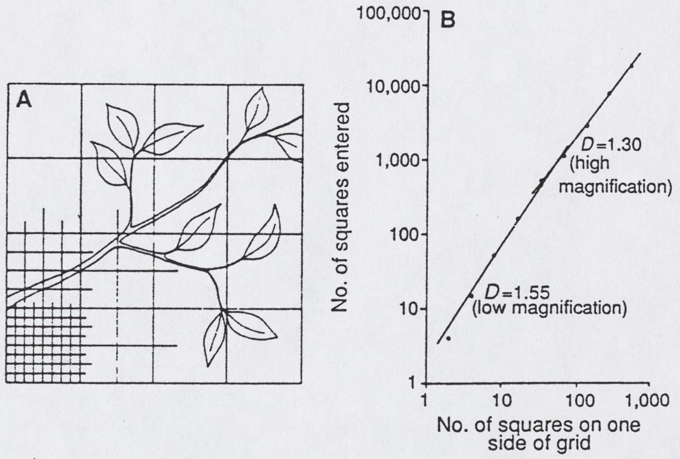

Fig. 3. (**A**) Photographs of plants at various magnifications were placed under a grid by Morse *et al.* (*21*). The number of squares entered by the outline of the plant were counted, starting with a coarse grid of two large squares on one side, then 2^n squares, with n varying from 2 to 6 or 7, depending on the grid size. For ease of representation, the plant's leaves in this figure are drawn flat; in reality they are oriented at all angles with respect to the grid. Also for clarity, the progressively finer divisions are only illustrated in one corner of the figure. The logarithm of the number of squares entered by the outline of the plant is then plotted against the logarithm of the number of squares along one side of the grid, as shown in (B). The slope of the line equals the fractal dimension, D. (**B**) Data gathered in this way for Virginia creeper, photographed without leaves in early spring. The twigs were photographed at one scale, then parts of the same twigs were rephotographed at a higher magnification, permitting D to be estimated at two levels of resolution.

Table 4. Estimated numbers of host-specific canopy beetles on *Luehea seemannii*, classified into trophic groups (*49*).

Trophic group	Number of species	Estimated fraction host-specific (%)	Estimated number of host-specific species
Herbivores	682	20	140
Predators	296	5	15
Fungivores	69	10	7
Scavengers	96	5	5
Total	1100+	—	160

of 160 species, or 44%). Most of these "rare habitat" species are specialists of marsh, sand dunes, bogs, or forest floors; wherever their habitat exists, they are predictably present (*36*). The category that is conventionally called "common" comes a close second, exemplified by species such as heather, *Calluna vulgaris*, or English oak, *Quercus robur* (58 of 160 species, or 36%). The remaining six categories are all less well represented, collectively accounting for only 20% of the total. The most frequent of these six are what are usually called "endemic rarities," specializing in one type of habitat but abundant in that habitat (14 of 160 species, or 9%); the Lady Orchid, *Orchis purpurea*, in Kent is an example. Other categories are uncommon, and one is unrepresented in the British flora: Rabinowitz *et al.* found no species with small populations in a variety of habitats but with a narrow geographic distribution. The absence of this category may reflect the small sample size, or it may reflect ecological mechanisms that are not yet fully understood.

We need more of these kinds of empirical studies of the multifactorial determinants of commonness and rarity (*37*). Not only do such studies illuminate fundamental questions about diversity, but they have practical implications for conservation biology. For instance, Table 1 helps justify the attention traditionally given by conservationists to "endemic rarities": not only are these species, with their narrow ranges and restricted habitat specificities, easily destroyed, but they are also numerically the most prevalent category of rare plants. Rabinowitz *et al.* speculated, moreover, that a better understanding of how endangered and extinct species are apportioned among their eight categories (or among other, alternative categories) may offer "clues about the causes of the endangered state" (*34*, p. 200).

How Many Living Species Have Been Recorded?

So far, this article has dealt with issues that must be resolved if we are ever to estimate the number of species in a given region, or on Earth, from basic principles. The second part of the article now reviews our current ignorance about the simple facts of how many species there actually are.

Living things may be divided into five kingdoms, distinguished by different levels of cellular organization and modes of nutrition. Two of these kingdoms, the prokaryotic monerans and the eukaryotic protists, comprise microscopic unicellular organisms, and together they account for something like 5% of recorded living species. The fungal and plant kingdoms represent roughly another 22% of species. The animal kingdom thus comprises the majority (more than 70%) of all recorded living species (*38*). Table 2 gives a rough account of how the species in the different animal phyla are apportioned according to the habitat of the adult creatures; each phylum represents a distinct body plan, with fundamental differences that distinguish it from all the others (*39*).

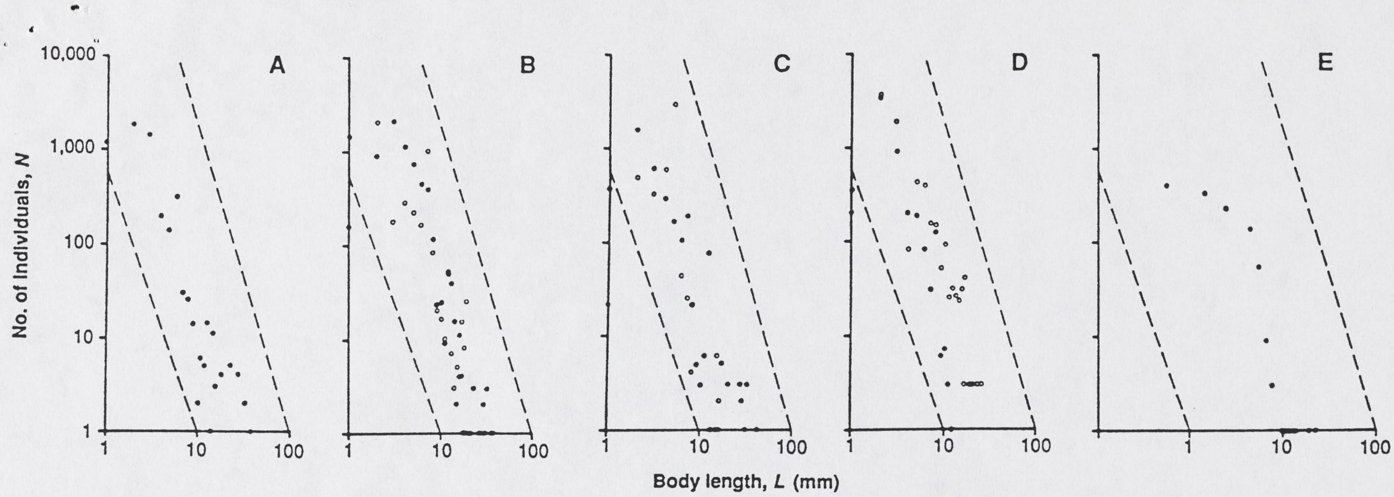

Fig. 4. Data plotted by Morse *et al.* (*21*) on the number of individual arthropods (mainly insects) of different body lengths, collected from vegetation: (**A**) understory foliage in primary forest in Costa Rica; (**B**) Osa secondary vegetation (solid dots) and Kansas secondary vegetation (open dots); (**C**) Tabago primary riparian vegetation (solid dots) and Icacos vegetation (open dots); (**D**) understory foliage in cacao plantations in Dominica (solid dots) and in Costa Rica (open dots); and (**E**) birch trees at Skipwith Common, North Yorkshire. The lower bound prediction that, for an order of magnitude decrease in body length, there should be a roughly 500-fold increase in the number of individuals, is indicated by the lower dashed line on each graph. The upper bound prediction—roughly 2000-fold increase for an order of magnitude decrease in body length—is shown by the upper dashed line.

Table 2 shows that most phyla are found in the sea, and more particularly in benthic environments; many phyla are found only in benthic habitats. On the other hand, by far the most abundant category of recorded living species is terrestrial insects. To a rough approximation and setting aside vertebrate chauvinism, it can be said that essentially all organisms are insects. Hutchinson (*40*, p. 149) has suggested that "the extraordinary diversity of the terrestrial fauna, which is much greater than that of the marine fauna, is clearly due to the diversity provided by terrestrial plants." Although it is true that in the sea vegetation does not form a structured environment (except close to shore) and that species generally have large geographical ranges (and the oceans are contiguous), closer examination suggests that there are subtle boundaries to dispersal in the sea and that latitudinal zonation is often more marked in the sea than on land (*41*). Viewing these questions in another light, Ray (*42*) has observed that although the sea contains only 20% of all animal species, it contains systematically higher proportions of higher taxonomic units, culminating in 90% or more of all classes or phyla (largely because all phyla are found in the sea, and the bulk of classes are exclusively marine). These facts make it plain that the factors influencing how many species there are in any one place—food web structure, relative abundance, species-size patterns, and so on—can operate differently in different environments and on different spatial scales.

Any interpretation of information about diversity, such as that summarized in Table 2, is clouded by uncertainties about how different two groups of organisms have to be before we call them different species, and by the fact that some taxa (for example, vertebrates) have been studied in vastly more detail than others (for example, mites). Even within very well studied groups, some workers recognize many more species than others. This is especially the case for organisms that can reproduce asexually; thus some taxonomists see around 200 species of the parthenogenetic British blackberry, others see only around 20 (and a "lumping" invertebrate taxonomist may concede only 2 or 3). Some strongly inbreeding populations are almost as bad, with "splitters" seeing an order of magnitude more species than do "lumpers" (*43*). At a more fundamental level, Selander (*44*) observed that different strains of what is currently classified as a single bacterial species, *Legionella pneumophila*, have nucleotide sequence homologies (as revealed by DNA hybridization) of less than 50%; this is as large as the characteristic genetic distance between mammals and fishes. Relatively easy exchange of genetic material among different "species" of microorganisms could mean that basic notions about what constitutes a species are necessarily different for vertebrates than for bacteria. But I think there are likely also to be systematic trends toward greater lumping of species of small and relatively less-studied organisms, and toward greater splitting as we approach the furries and featheries.

In Table 3, I attempt to give a rough impression of how the efforts of professional taxonomists and systematists are currently distributed among the major groups of organisms. Obviously the vertebrates, which comprise only 3% of all animal species, receive a disproportionate amount of attention. One result is that new birds continue to be found at the rate of about three species per year (against a total of around 8000 species), and new mammals at the rate of around one genus per year (against a total of around 600 genera), which contrasts with the possibility that there may be more than ten insect species for every one yet classified (*45*).

Setting all these reservations and biases aside, the total number of living organisms that have received Latin binomial names is currently around 1.5 million or so (*46*). Amazingly, there is as yet no centralized computer index of these recorded species. It says a lot about intellectual fashions, and about our values, that we have a computerized catalog entry, along with many details, for each of several million books in the Library of Congress but no such catalog for the living species we share our world with. Such a catalog, with appropriately coded information about the habitat, geographical distribution, and characteristic abundance of the species in question (no matter how rough or impressionistic), would cost orders of magnitude less money than sequencing the human genome; I do not believe such a project is orders of magnitude less important. Without such a factual catalog, it is hard to unravel the patterns and processes that determine the biotic diversity of our planet.

How Many Living Species Are There?

Until recently, the total number of species was thought to be around 3 million to 5 million. This estimate was obtained roughly as follows (*46*). For the species of mammals, birds, and other larger animals that are relatively well enumerated, there are roughly twice as many species in tropical regions as in temperate ones. The total number of species actually named and recorded is around 1.5 million, and two-thirds of these are found in temperate regions. Most of these are insects. But most insects that have actually been named and taxonomically classified are from temperate zones. Thus, if the ratio of numbers of tropical to temperate species is the same for insects as for mammals and birds, we may expect there to be something like two yet-unnamed species of tropical insects for every one named temperate species. Hence the overall crude estimate of a total of roughly three times the number currently classified, or around 3 million to 5 million.

This estimate is open to several questions. For one thing, the total includes relatively few species of bacterial, protozoan, and helminth parasites, largely because such parasites are usually studied in connection with economically important animal hosts. But it could be that essentially every animal species is host to at least one specialized such parasitic species (*47*), which would immediately double the estimated total. For another thing, the Acarina (mites), both tropical and temperate, are even less well studied than tropical insects; it was largely tropical insects that carried the estimate from the known 1.5 million to 3 million to 5 million, and mites could carry it significantly higher.

An indirect approach to the question of the number of species whose body size is small is through studies of species-size relations, such as that in Fig. 2. Figure 6 depicts a very crude estimate of the global totals of terrestrial animal species in different size categories (classified, on a logarithmic scale, according to characteristic body length); the data in Fig. 6 are the result of a multitude of rough and uncertain estimates (*18*). The dashed line indicates the scaling of numbers of species as L^{-2} (*20*); the fractal considerations reviewed in connection with Figs. 3 and 4 suggest the scaling might more appropriately be somewhere between $L^{-1.5}$ and L^{-3} (*48*). Whatever the detailed scaling relation at larger body sizes, it clearly breaks down for organisms whose characteristic body length is significantly below 1 cm. But these are exactly the same creatures—insects, mites, and the like—that have received relatively little attention from taxonomists. Because we lack a fundamental understanding of the size-species relation itself, there is no reason to expect a simple extrapolation of the scaling law for large sizes to estimate accurately the number of unclassified smaller species. It is, however, interesting that the total number of species obtained by extrapolating down to around 1 mm or so is in the range 10 million to 50 million.

A sounder basis for an upward revision of the estimated number of species comes from Erwin's studies of the insect fauna in the canopy of tropical trees (*49*). Using an insecticidal fog to "knock down" the canopy insects, Erwin found that most tropical arthropod species appear to live in the tree tops. This is not so surprising, because this is where there is most sunshine as well as most green leaves, fruits, and flowers.

Erwin's original studies (*49*) were on canopy-dwelling beetles (including weevils) collected from *Luehea seemannii* trees in Panama over three seasons. He found more than 1100 species of such beetles, distributed among the categories of herbivore, predator, fungivore, and scavenger as shown in Table 4. To use this information as a basis for estimating the total number of insect species in the tropics, one needs to know what fraction of the fauna are specific to the particular tree species or genus under study; unfortunately, there are essentially no data bearing on this point. Erwin estimated 20% of the herbivorous beetles to be specific to *Luehea* (in the sense that they must use this tree species in some way for successful reproduction) (Table 4); the overall answer is more sensitive to this guess than to the corresponding figures of 5%, 10%, and 5% for predator, fungivore, and scavenger beetles, respectively. In this way, one arrives at the estimate of around 160 species of canopy beetles specific to a typical tropical tree.

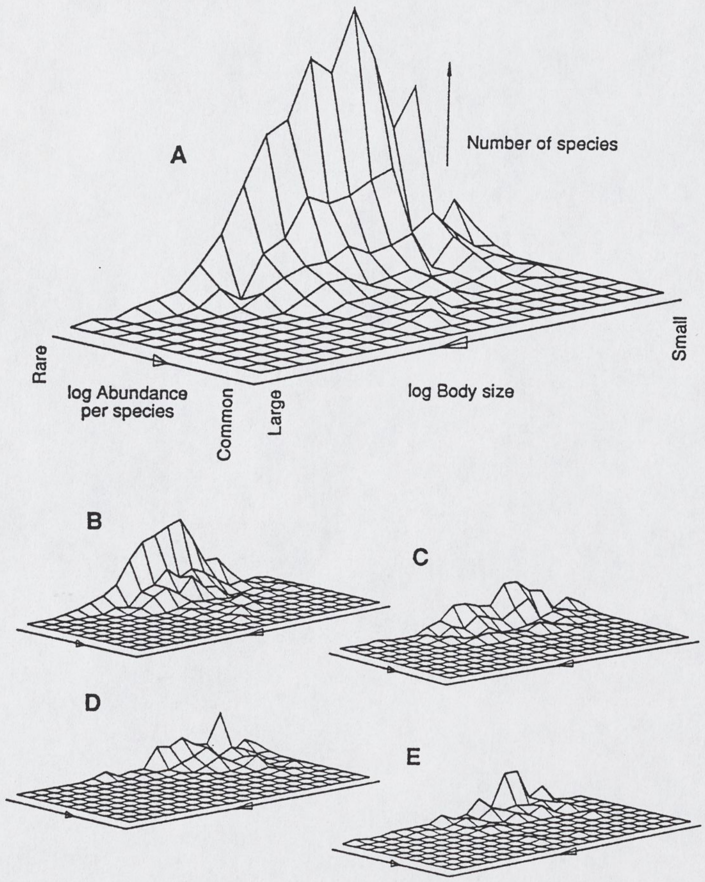

Fig. 5. (**A**) The height of each intersection is proportional to the number of beetle species that have a particular combination of body length [plotted logarithmically on a scale that extends from 0.5 mm, "small," to 30 mm, "large"] and abundance [plotted as logarithms to the base 2, on the conventional "octave" scale of Preston (*15*)]; for details, see (*29*). (**B** through **E**) The same information for the separate beetle guilds of herbivores, predators, fungivores, and scavengers, respectively (*29*).

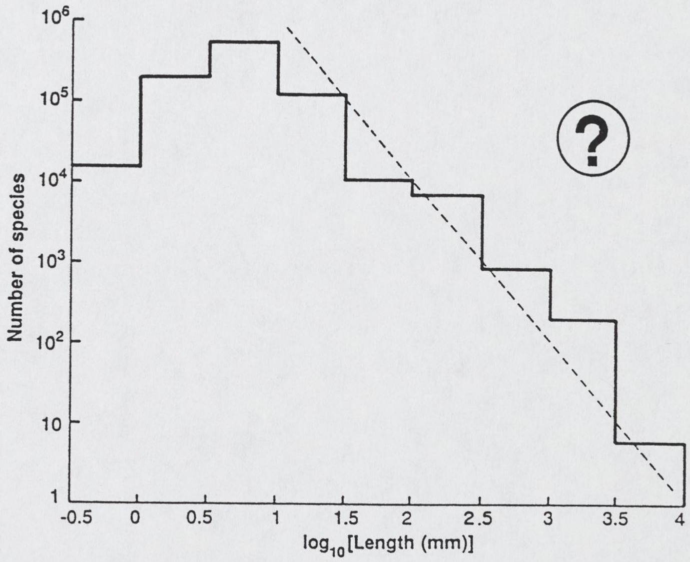

Fig. 6. A crude estimate of the distribution of number of species of all terrestrial animals, categorized according to characteristic length L. The dashed line indicates the relation $S \sim L^{-2}$, as in Fig. 2 (S is number of species) [after (*18*)]. The question mark emphasizes the crudity of these estimates and the inadequacy of the data for small size classes.

Several other assumptions are needed to pyramid this estimate of 160 host-specific species of canopy beetles per tree to 30 million species in total. Slightly simplified, the argument runs as follows. First, Erwin noted that beetles represent 40% of all known arthropod species, leading to an estimate of around 400 canopy arthropod species per tree species. Next, Erwin suggested the canopy fauna is at least twice as rich as the forest-floor fauna and is composed mainly of different species; this increases the estimate to around 600 arthropod species that are specific to each species or genus-group of tropical tree. Finally, using the estimate of 50,000 species of tropical trees (*50*), Erwin arrived at the possibility that there are 30 million tropical arthropods in total. This estimate has been widely cited, often without full appreciation of the chain of argument underlying it.

Although it is easy to cavil at each step in Erwin's argument, the work is important in providing a new and focused approach to the problem of estimating how many species there are. Erwin does not so much answer the question as define an agenda of research.

First, the overall estimate depends almost linearly on the necessarily arbitrary assumption that 20% of the herbivorous beetles are found only on one species or genus-group of tree; changing this number to 10% would halve the global estimate to 15 million species. I think it likely that insects feeding in the canopies of rainforest trees could be significantly less specialized in their use of food plants than are temperate insects, in order to help them deal with the sparse distribution of many tropical trees. Experiments that "knocked down" the canopy insect fauna from each of many neighboring trees of different species could shed light on these issues and provide a firmer basis for the estimates in the last column of Table 4 (*51*).

Second, the fact that 40% of taxonomically classified arthropod species are beetles is of doubtful relevance if, in truth, essentially all arthropods are unclassified tropical canopy dwellers. What we need to know is the fraction of the canopy fauna that are beetles. Again, this information could be obtained by systematic studies of the overall arthropod fauna in the canopies of a variety of tropical trees.

Third, the assumption that there are roughly two canopy species for each forest-floor species is also amenable to systematic study. Such studies should, in my view, reach below the forest floor into the soil, attempting to get a better idea of the species diversity of decomposing animals (including nematodes and other helminths) and other soil-dwellers.

More generally, I believe our ignorance of tropical mites—to name but one group—is at least as great as the ignorance about beetles and other arthropods that Erwin has exposed. These other groups may be similarly diverse. One proposal that is ambitious by ecological standards (although not by those in the physical sciences) is to assemble a team of taxonomists, with a comprehensive range of expertise, and then make a rough list of all the species found in one representative hectare in the tropical rain forest; it would be better to census several such sites (*52*). Until this is done, I will not trust any estimate of the global total of species.

Coda

For most of the history of life on Earth that is preserved in the fossil record, rates of extinction and rates of speciation have been roughly commensurate. If, however, we assume that something like half the extant species evolved in the last 50 million to 100 million years and that maybe half of all extant species will become extinct in the next 50 to 100 years if current rates of tropical deforestation continue, then contemporary rates of speciation are of order 1 million times slower than rates of extinction (*53*). Were speciation rates plotted as the y-axis on a graph 10 cm high, then on the same scale extinction rates would require an x-axis extending 100 km.

These circumstances give a special urgency to the kinds of studies called for above. Unlike essentially all other scientific disciplines, conservation biology is a science with a time limit, with the clock ticking faster as the human population continues to increase. We need to understand the world of living things for the same fundamental reasons that we need to understand the physics of the unimaginably small and of the unimaginably large. We also need such understanding to manage the biosphere in a sustainable way (which we do not appear to be doing at present) and to design rational strategies for preserving some habitats while exploiting others in ways that allow some fraction of the original flora and fauna to persist. I believe future generations will find it blankly incomprehensible that we are devoting so little money and effort to the study of these questions.

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The Diversity of Life

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The zoology of dreams is poorer than the zoology of the Maker. –Jorge Luis Borges

The history of life is traced through its four great revolutions: first procaryotic organisms, first eukaryotic cells, first multicellular organisms, and first cultural species. The magnitude of diversity has fluctuated widely through the agency of mass extinctions and bursts of adaptive radiation, concluding in the millions of species alive today—of which only 1.4 million have been given scientific names. A few headquarters of evolution—notably the tropical forests, coral reefs, and deep sea—have special significance in our story. As humankind takes control of the Earth's management, and of evolution itself, life approaches its fifth great revolution.

The past 100 years have seen a remarkable expansion in our knowledge of global biodiversity: how much there is, where it is concentrated, where it comes from, and how long it takes to create. Yet these key questions have been only partially answered. Despite the fact that the formal study of biodiversity began in 1753, with Linnaeus' inauguration of the binomial system of classification, the field remains intellectually young. Fewer than half the species of organisms have received scientific names, and only a minute fraction have been studied with any care. The principal generalizations about diversity are relatively new and in many cases subject to controversy. They all begin with the events in evolution that made diversification possible.

Evolution in Four Steps

Four great steps, occurring about a billion years apart, have profoundly altered the direction of evolution and added whole new layers of species in the energy pyramids of the ecosystems. The first was the origin of life itself about 3.5 billion years ago. The earliest known organisms were bacteria-like filaments and blue-green algae composed of prokaryotic cells, which lacked cell membranes, mitochondria, chloroplasts, and other organelles. The assembly of organelles into the eukaryotic cell was the second seminal advance. It required another 1.9 billion years, occurring no later than 1.4 billion years before the present. About 700 million years ago came the third step, the origin of the first multicellular animals. The earliest of these creatures known in the fossil record composed the Ediacaran fauna, named for the Ediacara Hills of South Australia where many of the first specimens were found. The animals were predominantly flat and soft-bodied. About 100 million years later, the first shelled creatures began to appear in substantial number and variety. Their appearance was accompanied by a rapid proliferation of body plans among species.

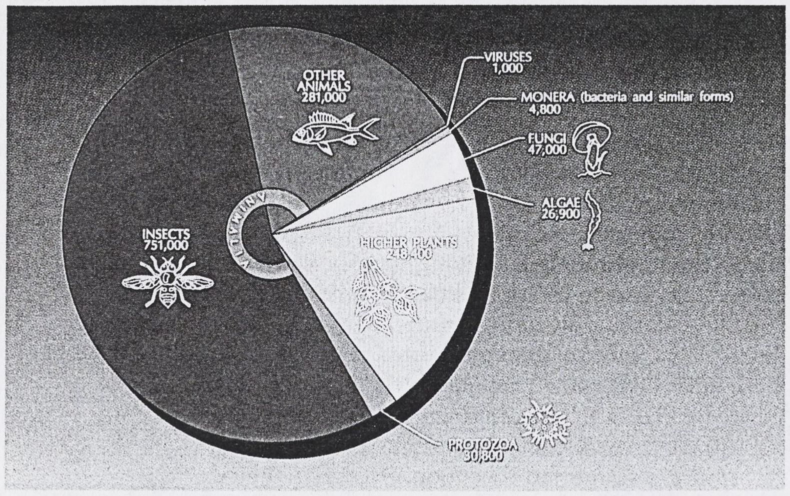
This period, spanning the transition from Precambrian to Cambrian times, was the great age of experimentation. Most kinds of animals persisted for only a short time, their *bauplan* never to be repeated in later eras. With the appearance of multicellular animals, complex food chains were created. Shelly animals, predators, and deep burrowers then rose to abundance. Their analogs and successors were destined to dominate the marine environment from that time on (McMenamin 1987, Morris 1987). During the Ordovician Period, about 450 million years ago, the first animals and bryophytic plants colonized the land (Retallek & Feakes 1987). By Devonian times, 375 million years before the present, terrestrial arthropods made their appearance, including mites and the most primitive wingless insects (Shear *et al.* 1984). In the Pennsylvanian Period, 100 million years later, a wide diversity of winged insects occupied the now dense forests of vascular plants. At this point all the major physical zones of the Earth had been conquered: water, land, and air.

The stage was now set for the fourth great step in evolution, the origin of Man. To put it this way is not to be unduly homocentric. The creation of a cultural species, in which most information is transmitted by open, creative language and learning, was a unique and profoundly important event for all of life. Culture energized a rapid and unique evolutionary change in our own species. Within less than 2 million years, from the appearance of the earliest "true" Man *Homo habilis* to the earliest *Homo sapiens* half a million years ago, the cerebral cortex enlarged 3.2 times, and an important architectural reorganization occurred in the speech-control centers of the parietal regions and memory banks of the forebrain. The rate of morphological change alone was possibly the most rapid in the history of life. It was driven by gene–culture coevolution, in which the genetically prescribed properties of cognition influence the evolution of culture, and cultural changes simultaneously guide genetic evolution by influencing which cognitive genotypes survive and reproduce. This coupled system of biological evolution and cultural evolution somehow accelerated the later stages of human evolution (Lumsden & Wilson 1983).

How Much Diversity Is There?

From literature sources such as the authoritative *Synopsis and Classification of Living Organisms* (Parker 1982) and new information provided by experts on various groups (see Acknowledgments), I have estimated the total number of living species known at the present time to be approximately 1,390,900. The breakdown of this diversity is presented in Figures 1 through 3. Several generalizations emerge from these data. First is the preponderance of multicellular organisms, which if genuine is an enduring heritage of the diversification that occurred during the Precambrian–Cambrian transition. Second is the far greater number of species—at least species known to science—on the land. The flowering plants (angiosperms) and especially the dicots prevail among the plants at the present time. The Animal Kingdom is dominated by medium-sized creatures between 1 and 10 millimeters in length, and these are overwhelmingly insects. When diversity is plotted against size of organism in the plants, the result is an inverted triangle, with relatively few known species at the bottom and the largest number near the top. The animals yield a diamond-shaped figure, with diversity swelling to the maximum near the middle of the size range. Going from the species to the phylum level (for example, all sponges taken together, all corals taken together, and so on), the greatest diversity is in the sea, where multicellular animal life originated and experimented during the Precambrian–Cambrian transition. But plant phyla are most diverse on land, where multicellularity evolved most vigorously during mid-Paleozoic times, following the golden age of animal experimentation. The prevailing plant forms in the sea remain algae, including forms resembling some of the early eukaryotic cells and filaments that dominated plant life a billion years ago.

Turning to the biomass of organisms in tropical forests (where most of the species of organisms live), an equally lopsided picture emerges. The vegetation consists overwhelmingly of flowering plants and especially dicots, with the monocotyledonous palms nevertheless holding their own among the trees and shrubs. Among the animals, insects again predominate—as detailed in Figure 4. And among the insects, the highly social forms—specifically termites, ants, social wasps, and stingless bees—make up an incredible 80 per cent of the biomass (Figure 5). These various proportions are probably not far from those occurring in grasslands and other major terrestrial habitats in most parts of the world. The proportions reflect the coevolution between the flowering plants and the insects that has occurred since early Mesozoic times, approximately 250 million years ago. Most of the plants depend on insects for pollination and seed dispersal, while a great majority of the insects depend on the plants for food and shelter. When mankind joined the social insects 2 million years ago, another important trend was completed: social life had come to largely dominate and manipulate the environment of the land.



ALL ORGANISMS: TOTAL SPECIES, 1,390,900

Figure 1. **The number of living species of all kinds of organisms known at the present time, according to major taxonomic group, are shown in this diagram. The actual number, including undescribed species, is much greater.**

Although the estimates on biomass are relatively firm, those on diversity are still very incomplete. In 1964 C. B. Williams, employing a combination of intensive local sampling and mathematical extrapolation, put the number of insect species at 3 million (and the number of living insects at any given moment at 10^{18}). During the last 20 years, systematists have described several new complex faunas in relatively unexplored habitats, such as the floor of the deep sea. They also began to employ protein analysis and ecological studies routinely, enabling them to detect many more "sibling species," in other words populations that are reproductively isolated from other populations but difficult to distinguish on the basis of museum specimens alone. As a result of these discoveries, a few writers began to put the world's total as high as 10 million species.

The estimates were raised yet again when Terry L. Erwin (1983) and other entomologists employed a technique that for the first time allowed intensive sampling of the canopy of the tropical rain forests. The number of species proved to be far greater than expected, because of unusually restricted ranges and high levels of specialization of different parts of trees. According to Erwin, a total of 30 million insect species may exist (mostly beetles). However, his estimate must be tested with many more samples from additional rain-forest localities before the true figure can be approximated with confidence.

The least that can be said is that biological diversity is still very incompletely mapped. We do not know the number of species even to the nearest order of magnitude. It could be as low as 3 million or as high as 30 million, or still more. Research is at an early stage in the exploration of not only tropical insects but also mites, nematodes, and other small organisms in the soil, and the complex invertebrate faunas of coral reefs and the deep sea. The present count of 3,000 bacteria must be drastically low. The niches into which these microorganisms can evolve are extremely numerous. Each of the millions of insect species, for example, is a potential host for specialized mutualistic and pathogenic forms. Other bacterial species live virtually incommunicado in very sparse populations, increasing to conspicuous numbers only under special conditions of nutrition, pH, and temperature. Thorough studies of local bacterial floras have been so few and far between as to leave bacterial diversity a mostly unexplored field.

Two Major Centers of Biological Diversity

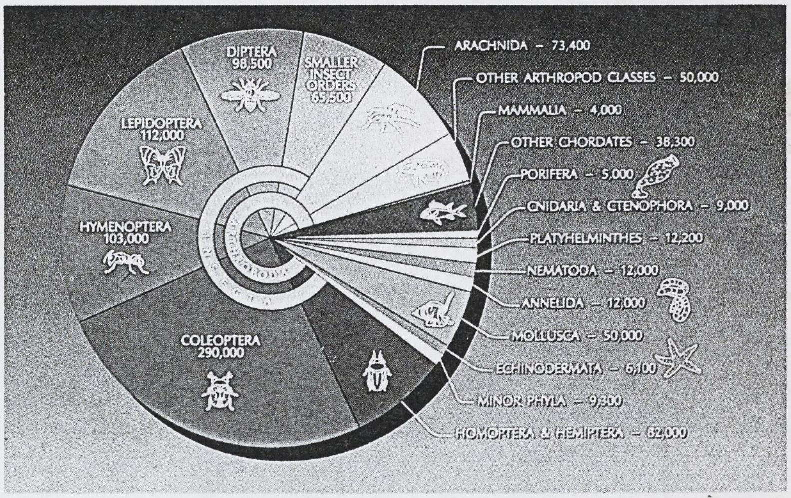
The tropical moist evergreen forests, or rain forests, occupy only 7 per cent of the land surface but contain at least half the species of organisms. In a few square kilometers in Ecuador or Malaysia can be found hundreds of species of birds, thousands of species of plants, and tens of thousands of species of beetles. Peter S. Ashton (personal communication) identified 700 species of trees in 10 selected hectares in Kalimantan; no more than 700 native tree species occur in all of North America. From a single tree in Peru, I identified 43 ant species belonging to 26 genera, approximately the same number as are in all of the British Isles (Wilson 1987a). The biologist studying the rain forest still addresses a mostly unknown terrain, much as did biologists a century ago.

The floor of the deep sea is another understudied reservoir of global biodiversity, containing as many as a million mostly undescribed species (H. L. Sanders personal communication). Many are annelid worms, molluscs, and echinoderms that scavenge detritus, which in turn falls from the upper lighted layers onto the vast abyssal plains. Others are limited to thermal vents that occur along the volcanically active subduction zones of the Pacific rim and mid-Atlantic ridge. The primary energy source of these abyssal sites is not detritus from above but bacteria that metabolize sulfur from subterranean sources. Each vent is an islandlike oasis with its own distinctive fauna. The commonest organisms include giant tube worms, colonial siphonophore "jelly fish," mussels, and galatheid squat crabs—most new to science and many constituting novel genera and even families of organisms (Childress *et al.* 1987). Elsewhere, cold seeps on the ocean floor possess a wholly different set of distinctive faunas, supported in this case mostly by methane-metabolizing bacteria (Turner 1985) (Figures 6 & 7). The organisms of the thermal vents and cold seeps, which were unknown before 1977, perhaps come as close as we will ever know to what life could be like on another planet. They demonstrate how resourceful organisms are when adapting to radically different environments.

How Species Are Created

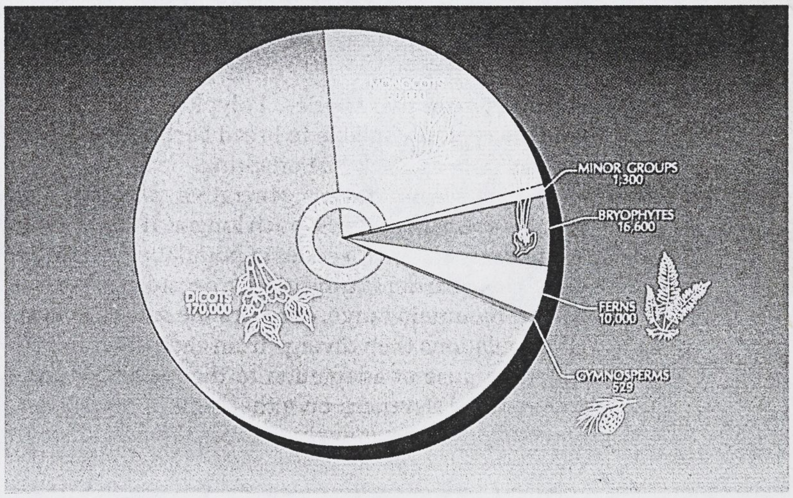
Organisms diversify through the formation of species, and all of classification is based on the species as the atomic unit. What, then, is a species? The modern "biological species concept" defines this unit as a population or series of populations within which gene flow occurs freely under natural conditions. This means that all of the normal, physiologically competent individuals at a given time are capable of breeding with all of the other individuals of the opposite sex belonging to the same species, or else they are linked to them genetically through chains of other breeding individuals. In brief, members of one species do not breed freely under natural conditions with those of other species. Tigers and lions hybridize when confined in captivity, but during historical times at least, they have never interbred where they lived together in the wilds of southern Asia. Hence, even though lions and tigers are capable of hybridization, they comprise two different species.

The biological species concept is the best ever devised, but it remains less than ideal. It works very well for most animals and some kinds of plants, but must be replaced with arbitrary divisions in many other plants (and in a few animals) where intermedi-



ANIMALS: TOTAL SPECIES, 1,032,000

Figure 2. **The number of living animal species known at the present time, according to major taxonomic group.**

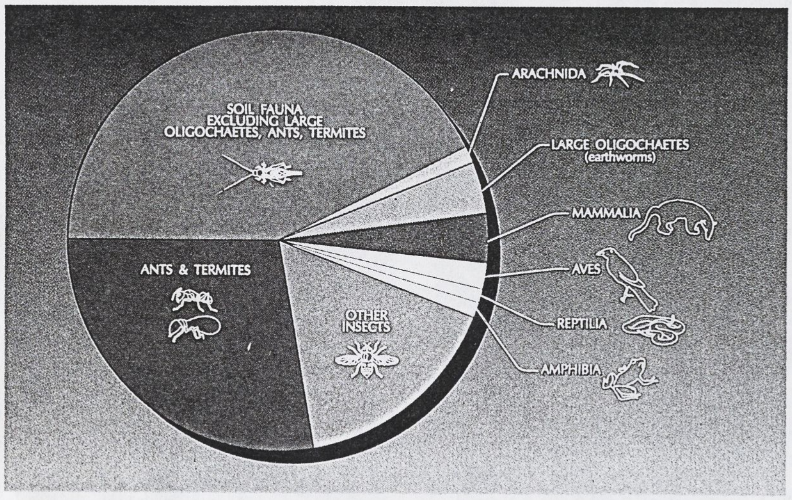


HIGHER PLANTS: TOTAL SPECIES, 248,000

Figure 3. **The number of living species of higher plants known at the present time, according to major taxonomic group.**

ate amounts of hybridization occur among natural populations, or where ordinary sexual reproduction has been replaced entirely or in part by self-fertilization or parthenogenesis.

New species are usually created in one of two ways. A large minority of plant species came into existence in one step, through polyploidy. This is a simple multiplication in the number of gene-bearing chromosomes, sometimes within a preexisting species and sometimes in the hybrids that infrequently



TOTAL ANIMAL BIOMASS

Figure 4. **The apportionment of biomass, measured in dry weight, among groups of animals in a rain forest near Manaus, Brazil. [source: Fittkau, E. J. & Klinge, H. 1973. On biomass and trophic structure of the central Amazonian rain forest ecosystem.** ***Biotropica*** **5:2–14]**

occur between two species. Polyploids formed this way are typically unable to breed back to the parent species to produce fertile offspring.

The second major generative process, geographic speciation, takes much longer. It starts when a single population (or series of populations) is divided by some barrier extrinsic to the organisms, such as a river, mountain range, or arm of the sea. The isolated populations then diverge from each other in evolution because of adaptation to the inevitable environmental differences on either side of the barrier. Since all populations evolve if given enough time, divergence between all extrinsically isolated populations must eventually occur. By this process alone the populations can acquire enough differences to reduce interbreeding between them should the extrinsic barrier be removed and the population again come into contact. If sufficient differences have accumulated by this time, the populations can coexist as newly formed species. If they have not occurred, the populations will resume exchanging genes; in other words, they will still belong to the same species.

Adaptive Radiation and Convergence

On different continents and islands and in different geological times, the relentless multiplication of species has created ecological communities that resemble each other in broad features. The origin of the species that make up these separated communities are often drastically different, yet the final products tend to be similar. Today the reefs of shallow tropical seas are made up largely of corals, which are colonial coelenterates that secrete calcareous skeletons. However, in the Tethyean Basin of Late Cretaceous times, prior to the formation of the Mediterranean Sea, they were composed of bivalve molluscs (Stanley 1987). In other places and geological periods they were built variously by calcareous algae, bryozoans, and other kinds of coral coelenterates. The proliferation of species into different niches of a community is called adaptive radiation. Thus coelenterates are said to have radiated into many niches, of which one is the formation of shallow-water reefs. On the other hand, a similarity acquired by species that occupy approximately the same ecological position but in difference places or times, such as reef building, is called evolutionary convergence.

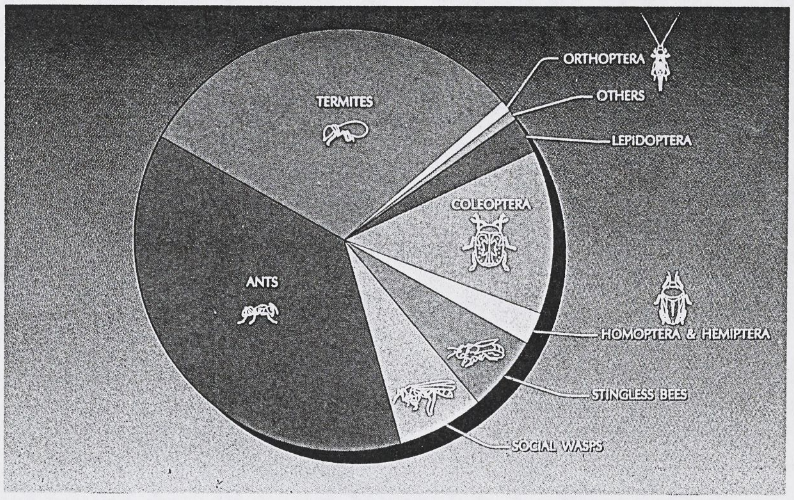
The dual processes of adaptive radiation and evolutionary convergence have been endlessly repetitive through time. Like a human dynasty, one group supplants another, radiates for a while, and then makes way for still another group. Paleontologists generally agree that more than 99 per cent of all evolutionary lines in geological history have become extinct (Raup 1979, 1981). In some cases, as in the complex lines that led from amphibians to reptiles and then to mammals, the ancestors of the new radiations were products of the previous ones. But in many other instances, such as the reef-building invertebrates, entire groups were supplanted by lines remote from their own, and often by invaders from other continents.

The most famous and instructive case is the triple adaptive radiation that produced the modern mammals. When the southern supercontinent of Gondwana broke up during the Mesozoic Era, two of the fragments were landmasses destined to become present-day Australia and South America. In the following 70 million years, separate radiations of mammals occurred on these two island continents, as well as on the northern "world continent" comprising Africa, Europe, Asia, and North America. Mammals were able to spread to some extent from one end of the world continent to the other.

The contemporary products of their evolution are our familiar dogs, antelopes, rhinoceroses, mice, and other warm-blooded animals. They are almost all descended from placental mammals, the females of which carry the young to an advanced stage of development in the uterus. In Australia, some two thirds of the mammal species are marsupials, in which the young are born while still very young and undeveloped; they then crawl into a pouch (the marsupium) located on the mother's belly and attach themselves to the mother's teats to complete their development. The degree of convergence that occurred during the simultaneous radiations on the two continents is astonishing. In some instances—for example, the flying squirrel (placental) versus the sugar glider (marsupial), the woodchuck (placental) versus the wombat (marsupial), and the placental versus the marsupial versions of the wolf and the mole—the external resemblance is so close that special instruction is needed to place a given species to the correct continent.

A third comparable mammalian radiation unfolded on South America, but in this case the plant-eating mammals were primarily placental and the carnivores marsupial (Figure 8). When South America and North America were connected by the rise of the Panamanian land bridge about 5 million years ago, the world-continent mammals largely replaced their South American analogs. At the present time world-continent elements, such as jaguars and deer, coexist with armadillos, prehensile-tailed monkeys, and other products of the early, autochthonous South American radiation.

My own favorite among adaptive radiations is that of the sharks. These fishes, after flourishing in the Paleozoic and shrinking to low levels of diversity in the Mesozoic, expanded once again to their present high level of about 350 species. Today they include some of the most diverse forms found in any animal group of comparable size. The smallest species, the cigar shark *(Squaliolus laticaudus)*, is only a foot long at maturity, and the largest, the plankton-feeding whale shark *(Rhincodon typus)*, reaches 60 feet. In between are gulper sharks, bramble sharks, wobbegongs, spurdogs, crocodile sharks, and others. Most look like conventional sharks but a few resemble variously salmon, eels, sawfish, and rays. The great white shark *(Carcharodon carcharias)* specializes to some extent on sea lions and other mammals. As a result it mistakes human swimmers for its normal prey. The cookie-cutter shark *(Isistius brasiliensis)* is a parasite of porpoises, whales, and large fishes such as bluefin tuna. Only about 18 inches long, it has a curving row of very long teeth on its lower jaw, which it thrusts into the bodies of its victims and twists to slice out 1- to 2-inch conical plugs of skin and flesh. My half-serious criterion for a fully developed adaptive radiation is that at least one species should specialize in feeding on other members of the same group. The sharks qualify very nicely: bull sharks, which can grow to 500 pounds, prey preferentially on smaller sharks of other species.



INSECT BIOMASS

Figure 5. **The apportionment of biomass among groups of insects in a rain forest near Manaus, Brazil. [source: Fittkau, E. J. & Klinge, H. 1973. On biomass and trophic structure of the central Amazonian rain forest ecosystem.** ***Biotropica*** **5:2–14]**

Extinction and Renewal

Both plants and animals have gradually become more diverse since the origin of multicellular life. The variety of terrestrial plants, measured by the mean number of species per flora, rose steadily after the conquest of the land until early Carboniferous times, then remained on a plateau for 220 million years. In Late Cretaceous times, buoyed by the rise of the flowering plants, floral diversity began a prolonged and steep rise until a few tens of thousands of years ago, when it reached the highest level ever at-

THERMAL-VENT COMMUNITY

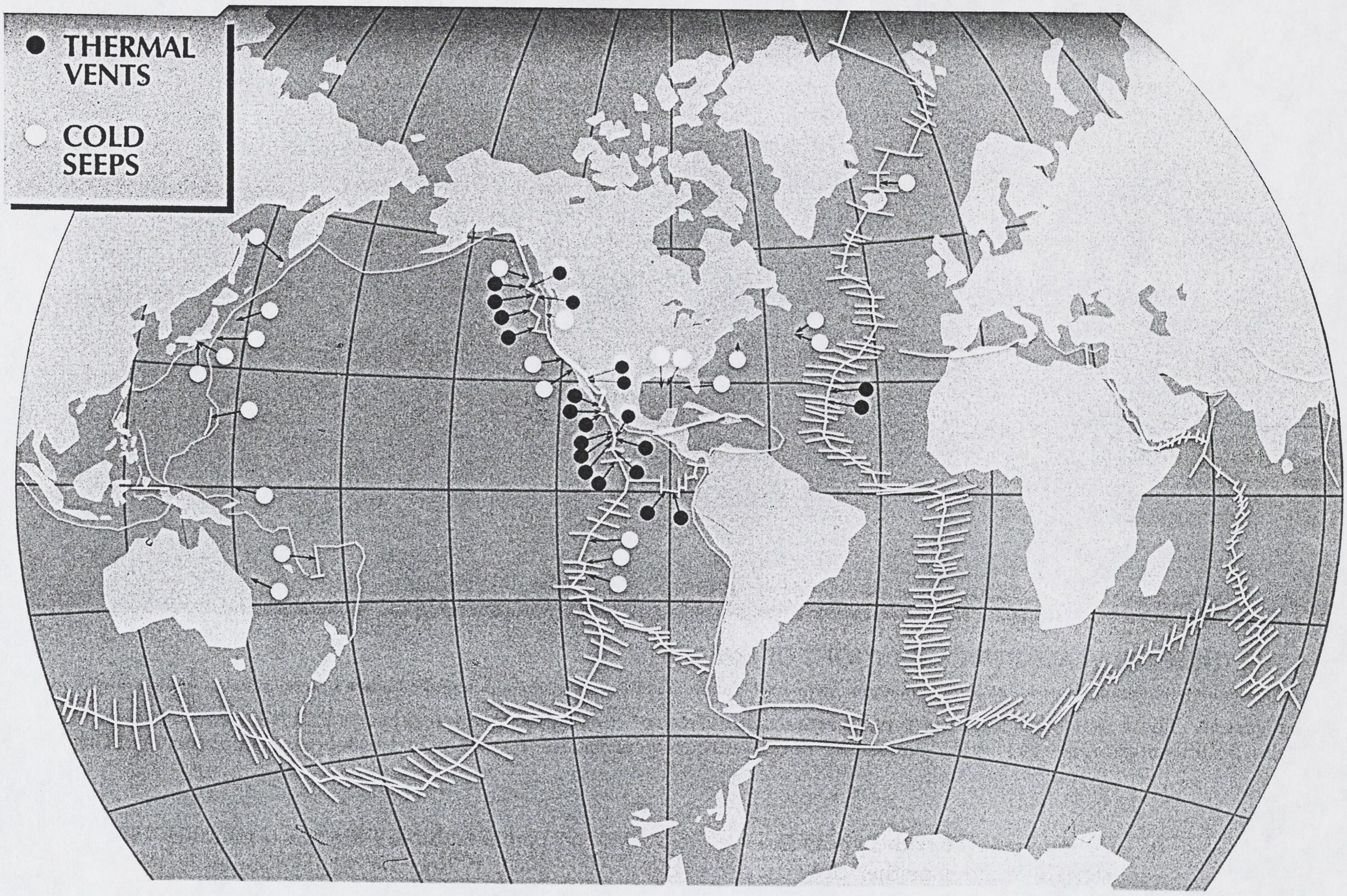
Figure 6. **This community, found in the Galápagos rift, includes *Riftia* tube worms, some as long as 8 feet. The rich and unique assemblages of the thermal vents and cold seeps were unknown before 1977. [photo: ©Al Giddings, Ocean Images]**

tained in geological history (Knoll 1986). It has begun to drop again through the massive alteration of natural habitats, especially the destruction of tropical forests. In parallel manner, marine animal diversity, which paleontologists have measured by various methods, rose to a plateau in the Devonian and Carboniferous, plummeted in the Permian and Triassic, and then rose again to a record peak in the late Tertiary (Raup & Sepkoski 1981, 1984) (Figure 9).

In short, global biological diversity is now at or close to its all-time high. Another way of putting it is that mankind came into existence in the most interesting time in which any sentient species could live. The living world arrived at this summit through an incessant turnover in principal organisms from one geological period to the next. Tree-like seed ferns and lycopsids dominated the Paleozoic forests. During the first part of the Mesozoic, they yielded to ferns, conifers, and cycads, which retreated in turn before the spread of the flowering plants. Among marine invertebrates, dominant elements of the Paleozoic Era included trilobites, brachiopods, and coelenterates. They were largely replaced by molluscs, protozoans, and non-trilobite arthropods during the Mesozoic Era.

Groups classified as high as orders and classes in the taxonomic scheme, such as cycads and brachiopods, turn over only across intervals of hundreds of millions of years. On the other hand, species, which collectively make up these higher taxa, persist for a much shorter period of time. Because of the proportionate richness of fossils in shallow marine deposits, the longevity of fish and invertebrate species living there can often be determined with a modest degree of confidence. During the Paleozoic and Mesozoic Eras, the average persistence of most fell between 1 million and 10 million years, that is, 6 million for echinoderms, 1.9 million for Silurian graptolites, 1.2 million to 2 million for ammonites, and so on (Raup 1984). These order-of-magnitude figures might not have broad generality. Terrestrial organisms are far less well known. Few estimates have been attempted, and hence different survivorship patterns might have been followed (although Cenozoic flowering plants, at least, appear to fall within the 1-million- to 10-million-year range). More importantly, a great many organisms on islands and other restricted habitats, such as lakes, streams, and mountaintops, are so rare or local in occurrence that they could appear and vanish through short periods of time without leaving any fossils.

In computing the longevity of species, paleontologists make a fundamental distinction between background extinction—the more or less continuous and seemingly random deaths of individual species here and there—and episodic mass extinction, which is the geologically relatively sudden and nearly simultaneous demise of large numbers of species. The "big five" of mass extinctions occurred, respectively, in the last Ordovician, Devonian, Permian, Triassic, and Cretaceous Periods (Figure 9). The Cretaceous episode is of course the most celebrated, because it included the end of the dinosaurs.



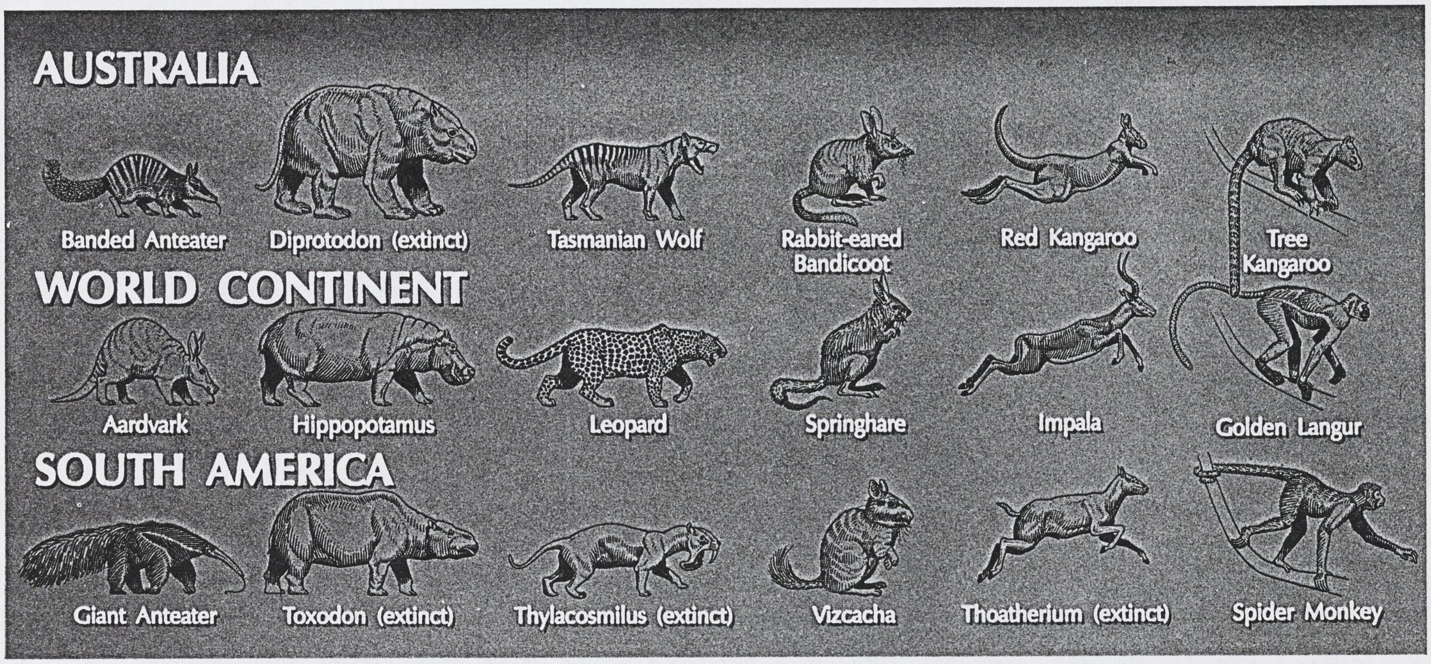
THERMAL VENTS AND COLD SEEPS

Figure 7. The distribution of thermal vents and cold seeps on the floor of the deep sea. These recently discovered sites contain dense concentrations of unusual organisms whose energy sources are sulfur- and methane-metabolizing bacteria. [source: Ruth D. Turner; data collected by the Deep Sea Biology Group of Woods Hole Oceanographic Institution]

But the most devastating occurred much earlier, at the close of the Permian. Between 77 and 96 per cent of all marine animal species were extinguished, as well as 52 per cent of the animal families. As David Raup (1987) said, "If these estimates are even reasonably accurate, global biology (for higher organisms, at least) had an extremely close call." For some 5 million years afterward, well into the early Mesozoic, diversity remained low, then began a climb that was never again to be so seriously threatened—never, at least, until the arrival of Man.

As shown in Figure 10, the Permian, Triassic, and Cretaceous peaks of extinction were interspersed by a series of smaller peaks. Taken all together, the episodes occurred at remarkably even intervals, which average 26 million years. Does a periodic cataclysm threaten humanity? We can relax a bit: the last episode was 11 million years ago, leaving us another 15 million years to prepare for the next.

Walter Alvarez and his coworkers, noting the presence of relatively large quantities of iridium and other rare elements at the Cretaceous–Tertiary boundary, proposed that the extinction spasm was caused by the strike of one or more large meteorites. This hypothesis, modified somewhat to include either meteorites or comets, has spurred an extraordinary growth of studies on the extinction process. In essence, a clear distinction has been drawn in theory between spasms due to Earth-bound changes (such as volcanic activity or reduction in the area of shallow seas) and spasms due to catastrophes of extraterrestrial origin (Officer *et al.* 1987).



THE THREE GREAT ADAPTIVE RADIATIONS OF MAMMALS

Figure 8. **These radiations have produced a remarkable series of convergences among species that fill the same major niche in Australia, South America, and the "world continent" of the northern hemisphere, respectively. [drawings: Theophilus Britt Griswold]**

Proponents of both hypotheses are locked in debate. The issue is neither clear-cut nor easily resolved. No high concentrations of iridium have been found at the geological boundary zones that mark other mass-extinction events, making it difficult to invoke the extraterrestrial model as a general explanation. Nor was the Cretaceous catastrophe as sharply demarcated as might be expected from a single bolide strike. The mollusc reef-builders declined drastically 3 million to 4 million years before the end of the Cretaceous. Dinosaur diversity also deteriorated during the concluding 2 million years; the *Triceratops* dominated the fauna, constituting about three quarters of all the large dinosaurs (Stanley 1987).

Of course, the boundaries of diversity loss could have been "smeared" by a sequence of bolide strikes over many thousands of years. Perhaps, on the other hand, the entrainment of more gradual climatic change by one strike caused the extinction of some groups before that of others (Weisburd 1986).

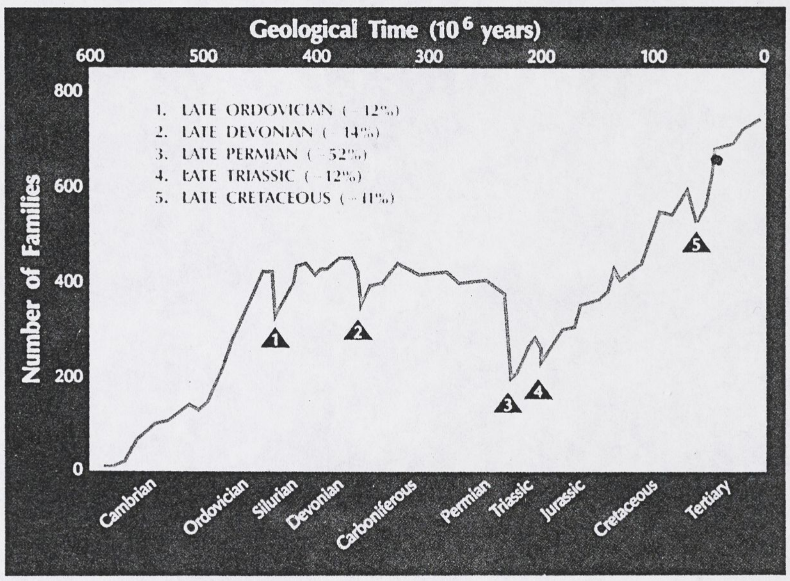
Whatever that prime cause of the mass extinction, without doubt some groups were affected more drastically than others. In the Cretaceous paroxysm, dinosaurs were hard hit, as were cephalopods, sponges, and a few other marine groups. In contrast, foraminifera, some insect groups, and flowering plants endured little loss (McKinney 1987, Whalley 1987, Wilson 1987b). McKinney has provided evidence that the groups most vulnerable to extinction during the five major episodes also suffered the highest background extinction rates during the periods in between. In other words, the environmental changes merely intensified the ordinary pattern of differential selection. However, even if this proves to have been generally the case, many major groups of organisms became *entirely* extinct while others survived with at least a few resistant species. The survivors were destined in many cases to spawn new adaptive radiations. In this way the great extinction spasms have had a major impact on evolution throughout the history of life.

The Future

Virtually all students of the extinction process agree that biological diversity is in the midst of its sixth great crisis, this time precipitated entirely by Man. The chief damage is due to the clearing of tropical forests, now proceeding at the rate of about 1 per cent of the total cover per year. The basis of this statement is not the direct observation of extinction in the threatened forests. To witness the death of the last member of a parrot or orchid species is a near impossibility. With the exception of the showiest birds, mammals, or flowering plants, biologists are reluctant to say with finality when a species has finally come to an end. Instead, extinction rates are usually estimated from principles of island biogeography: the areas of surviving habitats are related to the numbers of surviving species and the rate at which diversity is most likely to decline (Nitecki 1984, Soule 1986). Using calculations of this kind, Simberloff (1984) has projected ultimate losses due to the destruction of rain forests in the New World tropical mainland. If present levels of forest removal continue, he believes, the stage will be set within a century for the inevitable loss of 12 per cent of the 704 bird species in the Amazon Basin and 15 per cent of the 92,000 plant species in South and Central America.

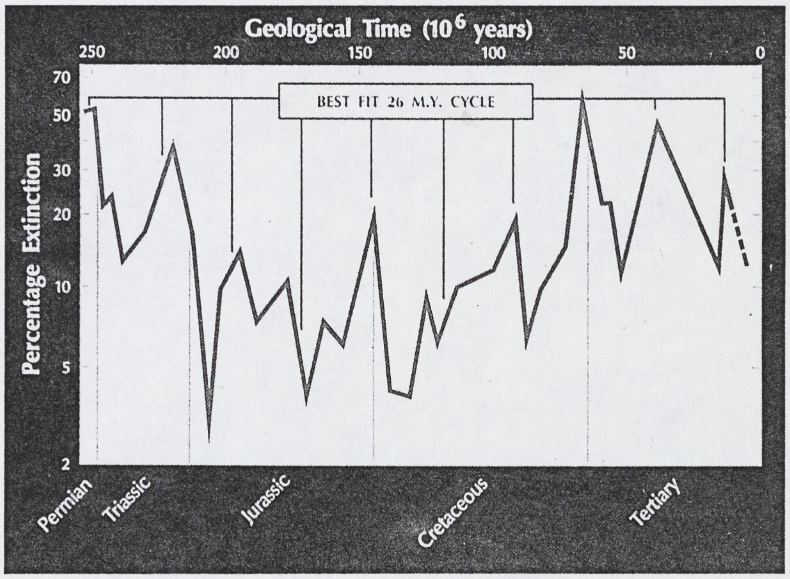
As severe as these regional losses are, they are far from the worst, because the Amazon and Orinoco Basins contain the largest continuous rain-forest tracts in the world. Less continuous tracts, which often harbor species found nowhere else, are far more threatened. An extreme example is the Pacific Coast forest of Ecuador. This habitat was largely undisturbed until after 1960, when a newly constructed road network led to the swift incursion of settlers and clear-cutting of most of the area. Now only patches remain, such as the 0.8-square-kilometer tract at the Río Palenque Biological Station. This tiny reserve contains 1,033 plant species, perhaps a fourth of which are known only from coastal Ecuador. Many are currently known only from a single living individual (Gentry 1982).

In general, the tropical world is clearly headed toward an extreme reduction and fragmentation of tropical forests, which will be accompanied by a massive extinction of species (Myers 1984, Raven 1980). Now less than 5 per cent of the forests are protected within parks and reserves, and even these are vulnerable to political and economic pressures: 4 per cent in Africa, 2 per cent in Latin America, and 6 per cent in Asia. In a simple system envisioned by the basic models of island biogeography, the number of species of all kinds of organisms can be expected to be reduced by at least half unless the destruction is slowed and halted. In other words, we will probably lose hundreds of thousands or even millions of species. Already, both the per-species rate and the absolute loss in number of species due to the current destruction of tropical forests (setting aside for the moment extinction due to the disturbance of other habitats) is likely about one to 10,000 times that prior to human intervention (Wilson 1987c).



MASS EXTINCTIONS

Figure 9. **The standing diversity through geological time of marine vertebrates and invertebrates. Clearly illustrated in these estimates are the rise of diversity to the Paleozoic plateau, the rise to the maximum just before historical times, and the five great extinction episodes, of which the late Permian (number 3) was the most severe. [source: Raup, D. M. & Sepkoski, J. J. Jr. 1982. Mass extinctions in the marine fossil record.** ***Science*** **215:1501–1503]**



EXTINCTION RECORD

Figure 10. **Extinction rates in species of marine organisms during the past 250 million years have apparently been periodic, with the average time between peaks being 26 million years. [source: Raup, D. M. & Sepkoski, J. J. Jr. 1984. Periodicity of extinctions in the geologic past.** ***Proceedings of the National Academy of Sciences, U.S.A.*** **81:801–805]**

I began this exposition with an account of the four great steps in evolution. The fourth of these, the origin of Man, will ultimately have the greatest impact on the world biota. We have become the greatest catastrophic agent since the extinction spasm that closed the Mesozoic Era 65 million years ago. But all that can quickly change. In less than an eyeblink of geological time, we have also discovered the origin of diversity, and we also possess enough knowledge to save and enrich it. How the human species will treat life on Earth, so as to shape this greatest of legacies, good or bad, for all time to come, will be settled during the next 100 years.

Acknowledgments

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BY THE NUMBERS

Freshwater Fish at Risk in the U.S.

Of all places on earth, rivers and lakes are the most dangerous for wildlife. Their natural ecology is segmented by dams and locks, their waters are diverted, and they are the principal depositories of civilization's wastes. It is therefore not surprising that aquatic species in the U.S. are at far greater risk of extinction than mammals and birds are. Of the 822 fish species native to American rivers and lakes, as many as 21 have become extinct since the time of the first European settlement, according to the Nature Conservancy in Arlington, Va., and its partners in the Natural Heritage Network. Their data show that another 297 species—36 percent of the total—are currently at risk of extinction. Other freshwater animals are in an even more perilous condition: 38 percent of amphibian, 50 percent of crayfish and 56 percent of mussel species are in jeopardy. Another 12 percent of mussel species are already extinct.

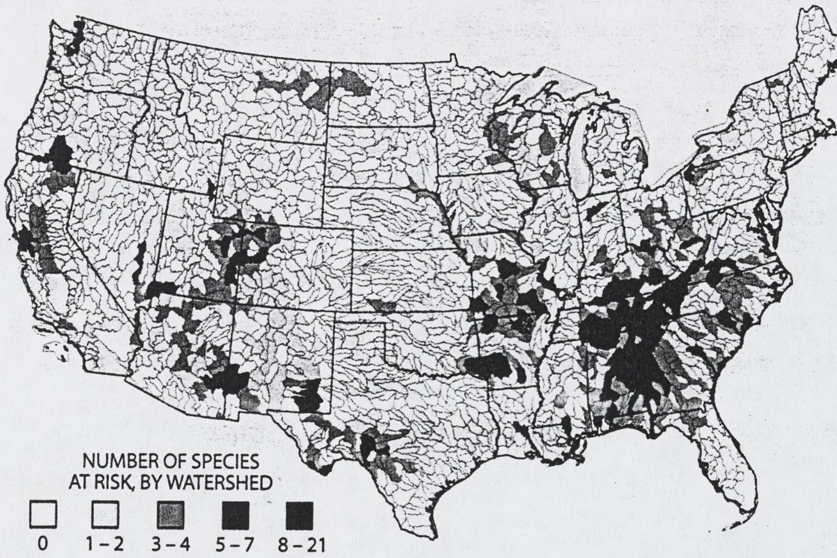
The three most important threats to freshwater fauna are agricultural runoff, dams and water diversion, and interference from exotic species (such as the flathead catfish, which was introduced in the Southwest and many other places for recreational fishing). Such alien species compete with native species and generally upset the balance of local ecologies.

Within the U.S. there is a wide variation in the status of fish, with the southern half of the country having far more imperiled species than the northern half; the large map below shows the number at risk in the 2,111 watersheds of the lower 48 states. The area of greatest concern is the Southeast, particularly the region stretching from Alabama and Georgia through Tennessee and Kentucky into southwest Virginia. This region is extraordinarily bountiful (*map at lower left*), rivaling the waters of tropical rain forests in the variety of its freshwater fauna. The large number of species throughout the Southeast stems from the highly diverse range of its ecosystems, including the Appalachian Mountains, the Appalachian Plateau, the Piedmont and the coastal plain. Also, this region, unlike the North, did not suffer the devastating effects of Pleistocene glaciation. Risk rates are higher in the Southeast than in the North (*map at lower right*) largely because of the effect that water projects have on the many localized fish species.

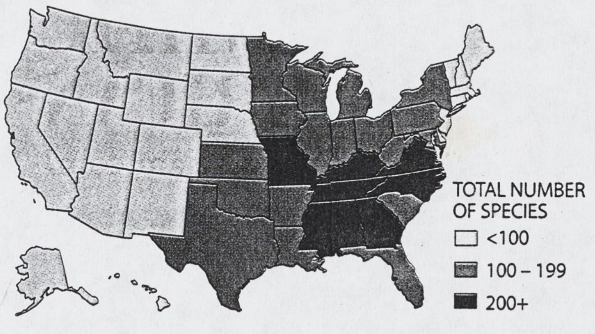
A second area of concern is the Southwest. This largely arid region, which has far fewer native freshwater fish species than the eastern part of the country, has been more severely affected by introduced species and water diversions. The result has been some of the highest risk rates recorded. In California, 42 percent of the 67 native fish species are at risk, and in Arizona the rate is an astonishing 63 percent.

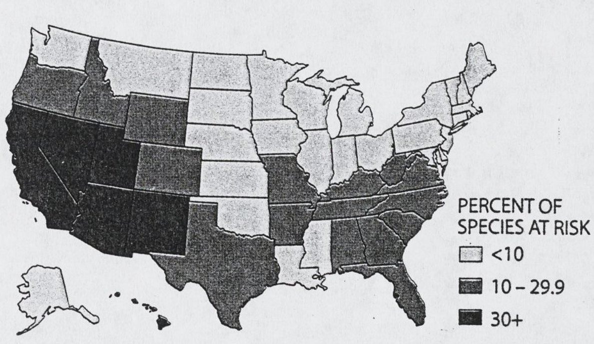
Another contributor to the high rates in some western states, such as California and Nevada, is the large number of species that have a limited range of habitat. An example is the desert pupfish, which is restricted to isolated and often vulnerable desert springs. Species with limited ranges also account for the high numbers of fish species at risk in the Ozark Plateau of northern Arkansas and southern Missouri and in the Klamath region of northern California and southern Oregon.

—*Rodger Doyle* (*rdoyle2@aol.com*)



SOURCE: The Nature Conservancy and Natural Heritage Network in cooperation with the Association for Biodiversity Information. All data are from 1997; excluded are species not native to their areas.





RODGER DOYLE

Extinction: Are Ecologists Crying Wolf?

Some contrarian critics argue that doom-laden prophecies of mass extinctions are based on assumptions that have modest scientific support and are wide open to question

IN 1979, NORMAN MYERS, A NATURALIST IN Oxford and Nairobi, published *The Sinking Ark*, the first prominent example of a now familiar genre—a book warning that the world could "lose one-quarter of all species by the year 2000." Although the danger extended from the whales in the frigid North Pacific to the elephants of the hot African savannah, Myers, like most of those who followed him, focused on tropical forests, the earth's most prolific and diverse biological communities. Claiming that these ecosystems—the home of perhaps one-half of the world's species—were being clear-cut at frightening speed, Myers warned that the ensuing loss of habitat would trigger "an extinction spasm accounting for 1 million species."

In public relations terms, such alarms were amazingly successful: Within a decade public concern had risen to the point that Madonna headlined a rock benefit called "Don't Bungle the Jungle." And estimates of the peril continued to rise. In this issue of *Science* (p. 758), biologists Paul Ehrlich of Stanford and E.O. Wilson of Harvard warn that biodiversity is in such danger that the United States must "cease 'developing' any more relatively undisturbed land" as but a "first step" to a solution. And that doesn't even touch the measures necessary in Third World nations, whose leaders must set aside vast reserves of land at considerable risk to the aspirations of their impoverished people.

That sounds like an awfully severe prescription. But don't make the mistake of thinking Wilson and Ehrlich represent an extreme or fringe point of view. Indeed, according to some critics, Wilson and Ehrlich are representatives of an exaggerated and distorted "bio-dogma" that runs the risk of impeding solutions to tropical forest deforestation—which all sides agree is a severe problem. Among those critics of orthodoxy is Ariel Lugo of the U.S. Forest Service's Institute of Tropical Forestry in Puerto Rico, who has been documenting the effects of deforestation there for a decade. Lugo thinks it's unfortunate that this bio-dogmatism has become entrenched because, he says, "no credible effort" has yet been made to pin down the scientific assumptions behind the mega-extinction scenario. "The fundamental problem that scientists are not able to answer yet is the relation between area lost and species made extinct," he argues. "But if you point this out, people say you are collaborating with the devil."

Lugo is one of a small group of scientists who disagree with the standard view of tropical forest extinction, and hence with the mega-extinction scenario as a whole. Although none is sanguine about humanity's disturbance of the Amazon, all believe that over- or misstating the problem endangers both the credibility of science and the effort to preserve biodiversity. "Wilson may be right, and that's very terrible," says Michael Mares, a zoologist at the University of Oklahoma. "But we should *know* he's right before making these wild demands, and we simply don't right now."

The most prominent of the naysayers is economist Julian Simon of the University of Maryland—a libertarian and nonstop controversialist who has long enraged advocates of population control by arguing that the world can support an almost infinite number of people, because substitutions and technological innovations make resources more plentiful. (In a typical puckish stunt, Simon bet Ehrlich 10 years ago that the world was not running out of resources—and the proof was that any commodity Ehrlich named would actually be cheaper in a decade. Ehrlich picked five metals; Simon won.)

In regard to biodiversity, Simon has argued since 1986 that the widely touted estimates of future extinction rates have no empirical basis whatsoever. Indeed, in two recent lists of extinction assessments—one compiled by Lugo, the other by Richard Tobin, a political scientist at SUNY-Buffalo—only four of 22 predictions came with sufficient explanation to permit independent examination. All of the rest provide anecdotal support—or none at all.

Even one prominent conservationist—who demanded anonymity, explaining that "they'll kill me for saying this"—admitted that "the lack of data does worry me." He then added: "I'm absolutely sure we're right, but a gut feeling isn't much backup when you're asking people all over the world to change their lives completely."

Moreover, the minority critics insist the "doom-and-gloom" scenarios contradict each other. Commentators such as Myers envision the disappearance of a quarter of the earth's species by the end of the century, whereas Ehrlich and Wilson conservatively figure the loss at between 2% and 3% in the same period—an order-of-magnitude discrepancy of the sort that one U.S. Office of Technology Assessment report concedes has "called into question the credibility of all such estimates."

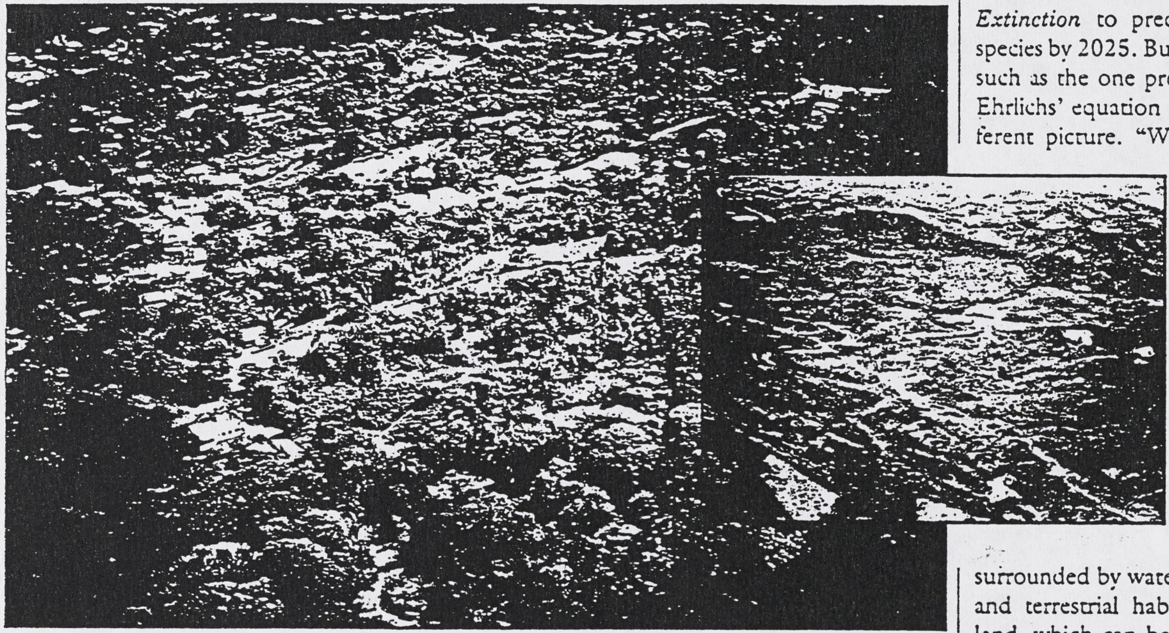
In reply to these criticisms, Wilson agrees that "of course" more data are needed. But, he says, the imminence of the extinction problem, particularly in tropical forests, is "absolutely undeniable." There are "literally hundreds of anecdotal reports." He adds

CRITICS TAKE ON THE "BIO-DOGMA"

	Assumption	Criticisms
Habitat loss	Most predictions of species loss are based on using islands as a model.	Mainland territories behave differently from islands—if original habitat is lost, species may escape into bordering areas. Data on habitat loss are frequently misleading.
Species-area curve	Current models of the relation between species and geographic area imply that an infinite increase in area implies an infinite increase in the number of species.	Critics argue that, in fact, the curve levels off at its upper reaches. Therefore, habitats on the upper part of the species-area curve can be reduced without substantial species loss.
The number of species	During the 1960s, researchers realized the incredible biological diversity of tropical forests and estimates of the number of species shot up—leading Wilson and Ehrlich to posit that 100 million species may live on Earth.	In fact, taxonomists have managed to name only 1.4 million species, and the actual total is a matter of speculation. Catastrophical estimates of extinction are based in large part on species no one has ever seen.

with some heat: "Believe me, species become extinct. We're easily eliminating a hundred thousand a year."

Part of the reason we don't have a clearer idea of extinction rates lies in the difficulty of estimating them. Serious efforts to calculate those rates hinge on the "species-area curve," which is based on the simple observation that



Comeback. *An area of Puerto Rico, deforested in the early 1900s, supports a rich growth of trees today.*

every community of species needs a habitat. The larger the habitat, the more species it can support. In the 1960s, Wilson and the late Robert H. MacArthur tallied the number of species on islands of various sizes, eventually constructing what is now known as the theory of island biogeography. The theory is usually summed up by the rule that N, the number of species, is proportional to $A^{.27}$ where A is the area. Extinction curves are calculated by inverting the relationship: treating habitats as "islands" and asking what happens to species as the island shrinks. Clearly, if a habitat drops below a minimum size, the community as a whole will cease to exist. But how fast does this take place? How much room is there for recovery? "The rule that is followed for teaching purposes," Wilson says, "is that for every 90% loss in area, the number of species that can live indefinitely there is cut by one-half."

In other words, the consequences of cutting down 90% of a tropical forest will be a forest of one-tenth the size with half as many species living in it—a scenario, Wilson stresses, that minimizes the damage. "Imagine in your mind an area of rain forest in southern Surinam. Now imagine cutting into the edge of it and reducing it 90%. You get that fall toward one-half in a system in which species are widespread. But if species are highly localized in their distribution, the loss will be far higher. If all species are in small, local, endemic communities, then the percentage loss of species will approach the percentage loss of area."

This is the point at which the skeptics open their assault on accepted wisdom. "The theory of island biogeography was originally developed to model what happens to the size of animal populations on islands," Lugo says, but "deforestation and extinction are entirely different." To get extinction rates from the island theory, he notes, requires three key assumptions: the rate of habitat loss, the shape of the species-area curve, and the absolute number of species. And all three are wide open to question, the critics say.

■ *Habitat loss.* Deforestation statistics, especially for the Amazon delta, are frequently misleading. According to Thomas Lacker, director of the Archbold Tropical Research Center at Clemson University, Brazilian government deforestation figures are for a political unit called "Amazonia," which rain forest advocates take as equivalent to rates of deforestation. But Amazonia consists of several types of forest and a large expanse—more than a third of the region—of savannah (*cerrado*) and semidesert (*chaco*). "The cerrado and chaco are being destroyed at a much faster rate than anything else," Lacker says. "The rate at which they're being gobbled up by soybean plantations is staggering. Then comes the dry forest, and last is the moist forest. So the actual wettest forest, which is what most of the attention is focused on, is not being hit as much as people sometimes think."

Figures from Cleber Alho, director of the Brazilian branch of the World Wildlife Fund, back him up. In figures sent to *Science* from his office in Brazil, Alho calculates the rate of actual forest clearing at 0.5% a year—a figure he concedes is "horrible," but which is half the size of what's usually cited. Ehrlich and his wife, biologist Anne Ehrlich, made use of the higher annual rate of 1% and an exponential function in their well-known 1981 book *Extinction* to predict a near-total loss of species by 2025. But plugging a lower figure, such as the one provided by Alho, into the Ehrlichs' equation provides a startlingly different picture. "What's going on is bad," Mares says. "But we have more time and room than the doomsayers let on."

Second, as the critics point out, deforestation is only roughly equivalent to actual habitat loss. Island biogeographical calculations assume that nibbling into a forest is like cutting off a piece of an island. But islands are surrounded by water, a hostile environment, and terrestrial habitats are surrounded by land, which can be entirely different. In an address before the National Forum on Biodiversity in 1986, Lugo pointed out that according to the only available study of the rate of increase in tropical secondary forests, almost half of the 11.3 million hectares of virgin tropical forest cut annually were turned not into wasteland—the equivalent of water in biogeographical calculations—but secondary forest. Another million hectares of secondary forest was created through reforestation or natural regeneration. Secondary forests are poorer, less diverse ecosystems than virgin forests, he said, but they are not necessarily disasters. (His audience did not appreciate hearing what might be considered good news—"I almost got eaten alive," Lugo says, with one eminent conservationist "yelling at me in the cafeteria of the Smithsonian.")

■ *The species-area curve.* Patrick Kangas, of the University of Maryland, on the other hand, critiques current views about the species-area curve, which is supposed to explain the relationship between an area available for wild populations and the number of species that area can support. At present, the exponential relation derived from the island studies of Wilson and MacArthur means that an infinite increase in area implies an infinite increase in species number. ("The species number increases smoothly with area up to the largest area you can look at," says Jared Diamond, a physiologist and ecologist at UCLA.) But according to Kangas, the apparent increase in number of species is a trivial consequence of the fact that a large area will contain a large number of ecosystems. As biologists cross borders from one community to another, they register sudden influxes of new species; this, he says, tells you nothing except many ecosystems have many species.

What is more important is the shape of the curve *within* a single community—and that, he says, is a very different matter. "There's a finite number of species within any community type," he says. "As you continue to move out, the number levels off." Further increase in area, in sum, does not produce concomitant increase in diversity. The result, the critics argue, is that habitats on the upper, flatter part of the species-area curve can be reduced without substantial immediate species loss—and hence, some of the habitat destruction we're now seeing in the world may not, in fact, translate into any loss of species.

When Kangas first explained his views at the International Congress of Ecology in 1986, he joined the select club of scientists who have been attacked in scientific articles for papers that have not yet been written. And, he says, he continued to be vilified for some time. "Please don't say I'm in favor of cutting down the rain forests," he asks from Belize, where he is doing fieldwork. "Because I'm absolutely not. But I think we've got ourselves into the position of following some kind of orthodoxy, rather than following the science."

■ *The number of species*. The problems of estimating habitat loss and computing the species-area curve are daunting enough. But there's an even bigger, more fundamental problem for those who are raising the alarm about extinction: science's taxonomic ignorance. Dennis Murphy, director of the Center for Conservation Biology at Stanford, says flatly, "Nobody knows how many species there are." As a result, those who prophesy the end of half of the world's species find themselves in the awkward position of predicting the imminent demise of huge numbers of species nobody has ever seen.

"Until the 1960s," Murphy says, "we thought there were maybe 3 or 4 million species, of which we had catalogued a million. Then people began to realize the incredible diversity of tropical forests, and guesses started shooting up." On the basis of new sampling techniques, Terry Erwin of the U.S. National Zoo calculated that there are 30 million species of insects; recently, mycologist David Hawksworth reckoned that there are 1.5 million types of fungi. And no scientist has even a guess at how many microorganisms remain to be added to the tally, a situation that led Wilson and Ehrlich to posit that the number of species may be close to 100 million. In the meantime, they note, taxonomists have managed to award scientific names to about 1.4 million species, less than 2% of what they argue is the total. Noting that the world's supply of taxonomists is far too small for the task of tallying the world's species, Wilson and Ehrlich call for a kind of national biodiversity project.

"Believe me, species become extinct. We're easily eliminating a hundred thousand a year."

—E. O. Wilson

And without such a national—perhaps international—effort, knowing how many species are going extinct will be, as Kangas puts it, reminiscent of the question of what sound a tree makes if it falls in the forest but there's no one around to hear it. If species are not discovered in the future, one cannot be sure whether they became extinct or never existed in the first place. As a result, Kangas says dryly, the "whole business is unfalsifiable, and everyone in science knows what a mess unfalsifiable theories are."

Questions such as these can best be answered by resorting to empirical evidence. And here, critics argue, the data for the mega-extinction scenario is at best ambiguous. One source of information is the study of isolated communities, such as solitary mountaintops or desert oases—and those have tended to confirm the laws of island biogeography. "One of the famous examples is a mountain ridge in Ecuador," Wilson says. "In a relatively small ridge of a few square kilometers, they found something like 90 species of plants found nowhere else. Between 1978 and 1986, farmers cleared the ridge, and extinguished most of the species in one shot."

Diamond, for his part, examined an isolated forest reserve in Java. Comparing bird species in the 1980s to those listed by a resident bird watcher in the 1930s, he found that the square-mile reserve had lost more than half. "Bird extinction rates are obviously very different from those of other taxa," he says. "They're highly vulnerable to habitat change. But the implication was clear."

But other measurements of larger, less isolated ecosystems—communities perhaps more representative of large rain forests—have yielded different results. "Look down at the eastern United States the next time you fly over it," Mares says. "It used to be solid forest all the way to the Mississippi. Now it's patches of isolated forest, exactly what we fear will happen to the tropics. But we didn't have a massive die-off." Rain forests are different than temperate forests, he agrees, but the evidence from the United States suggests that simple predictions from species-area curves are "glib."

Most champions of tropical ecosystems say deforestation is well-nigh irreversible because forest soils are nutrient-poor: Food stocks are held mostly in living creatures and are quickly recycled. In clearings created by logging, rain washes away all value from the soil, leading to a barren, brick-hard surface that will remain for centuries. Extinction is thus the likely alternative. But evidence from Puerto Rico suggests this alarming scenario is not the only alternative. In a frightening example of environmental degradation, the island, one of the few tropical places where long-term biological records have been kept, was almost completely stripped of virgin forest at the turn of the century. Yet it did not suffer massive extinctions. Even birds lost only seven of 60 species—a painful, even unacceptable, total, but not an eco-catastrophe. Now, 90 years later, Puerto Rico is thickly covered with trees.

As Lugo concedes, this relative good fortune may have occurred because the native fauna, evolved through many hurricanes, was adapted to living in a disaster zone. But, he argues, the lesson is clear. "We are asking Latin countries to go to enormous efforts on the basis of a scientific theory that is full of uncertainties," he says. For Kangas, the key issue is a practical one. "For policy questions," he says, "the essential point is that not all forest-clearing is the same." And conservationists need to offer decision-makers "low-impact alternatives" rather than issuing blanket predictions of disaster. Adds Mares, "If we keep saying things are going to go extinct tomorrow and they don't, people are going to stop believing us. And that will hurt us the day after tomorrow, when they may actually go extinct." ■ CHARLES C. MANN

Charles C. Mann is a free-lance writer living in New York.

Article

Biodiversity Studies: Science and Policy

Paul R. Ehrlich and Edward O. Wilson

Biodiversity studies comprise the systematic examination of the full array of different kinds of organisms together with the technology by which the diversity can be maintained and used for the benefit of humanity. Current basic research at the species level focuses on the process of species formation, the standing levels of species numbers in various higher taxonomic categories, and the phenomena of hyperdiversity and extinction proneness. The major practical concern is the massive extinction rate now caused by human activity, which threatens losses in the esthetic quality of the world, in economic opportunity, and in vital ecosystem services.

From Linnaeus to Darwin to the present era of cladograms and molecular evolution, a central theme of biology has always been the diversity of life. A new urgency now impels the study of this subject for its own sake: just as the importance of all life forms for human welfare becomes most clear, the extinction of wild species and ecosystems is seen to be accelerating through human action (*1*). The dilemma has resulted in the rise of biodiversity studies: the systematic examination of the full array of organisms and the origin of this diversity, together with the methods by which diversity can be maintained and used for the benefit of humanity. Biodiversity studies thus combine elements of evolutionary biology and ecology with those of applied biology and public policy. They are based in organismic and evolutionary biology in the same manner that biomedical studies are based in molecular and cellular biology. They include the newly emergent discipline of conservation biology but are even more eclectic, subsuming pure systematic research and the practical applications of such research that accrue to medicine, forestry, and agriculture, as well as research on policies that maximize the preservation and use of biodiversity. In biodiversity studies, the systematist meets the economist and political scientist. In this article we will present some of the key issues that newly link these two principal domains.

Species Formation

A rich medley of models has been constructed to account for the origin of species by reproductive isolation. Two broad categories have been substantiated by empirical evidence. The first is polyploidy, the multiplication of entire chromosome numbers within individual species or within hybrids of species, a process that isolates the new breed from its ancestor in one step. This instantaneous mode has generated 40% of contemporaneous plant species and a much smaller number of animal species (*2*). Of comparable importance is geographic (or allopatric) speciation, the origin of intrinsic isolating mechanisms in two or more daughter populations while they are isolated by a geographic barrier, such as a sea strait, desert basin, or mountain range. Evidence of this two-step process, which occurs widely in plants and animals, has been documented minutely, often to the level of the gene, in birds, mammals, and a few groups of insects such as drosophilid flies and butterflies (*3*).

The diversification processes of polyploidy and geographic isolation are generally appreciated because they follow an easily traced pathway of measurable steps. Other modes of speciation are more difficult to conceive and test, but this does not mean they do not occur widely. Perhaps the most common is nonpolyploid sympatric speciation, in which new species emerge from the midst of parental species even when individuals of both populations are close enough to intermingle during part of their life cycles. The dominant process of this category, at least the one most persuasively modeled and documented, is by intermediate host races. Members of the parental species feed upon and mate in the vicinity of one kind of plant; they give rise to an alternate host race that shifts to a second species of host plant growing nearby; the two races, thus isolated by their microhabitat differences, diverge further in other traits that reinforce reproductive isolation. Sympatric speciation may play a key role in the origin of the vast numbers of insects and other invertebrates specialized on hosts or other types of microhabitats. The early stages are difficult to detect, however, and few studies have been initiated in the invertebrate groups most likely to display them (*4*).

Certain forms of speciation can thus occur very rapidly, within one to several generations. And when species meet, they can displace one another genetically within ten or fewer generations, reducing competition and the likelihood of hybridization (*5*). A question of central importance is the impact of high speciation rates on standing diversity. Although the probability of extinction of species within a particular group at a particular place (say, the anole lizards of Cuba) eventually rises with the number of species, the number of species should increase with greater speciation rates at all levels up to equilibrium. But does it really? And if so, in which groups and to what degree?

Current Levels of Biodiversity

Also in an early stage, and surprisingly so, is the elementary taxonomic description of the world biota. At the present time approximately 1.4 million species of plants, animals, and microorganisms have been given scientific names (*1, 6*). Terrestrial and freshwater species diversity is greater than marine diversity. The

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overwhelming elements are the flowering plants (220,000 species) and their coevolutionary partners, the insects (750,000 species). The reverse is the case at the highest taxonomic levels, with all of the 33 living animal phyla present in the sea and only 17, or half, present on land and in fresh water (*7*).

Known species diversity is only a small fraction of actual species diversity, especially in the invertebrates and microorganisms. In this century the class Insecta has always been considered the most speciose group at the class level. As early as 1952, Sabrosky estimated that the number of living species is as high as 10 million (*8*). In 1982, Erwin found that beetle diversity in Neotropical trees, revealed in samples knocked down by insecticidal fogs, suggest far higher levels of insect and other arthropod diversity in tropical rain forests than had previously been estimated for the entire world fauna and flora (*9*). His figure, 30 million, was reached by extrapolating from counts of beetle species (1200) in a Panamanian tree species through estimates of total arthropod diversity per tree species to the percentages of species limited to each tree species to the total of tree species in tropical rain forests. Stork (*10*) reassessed this bold extrapolation, and in essence agreed with it, adding data of his own from Indonesian forests to produce a possible range of 10 to 80 million tropical forest arthropods. The most sensitive parameter remains the degree to which species of beetles and other arthropods are found uniquely on individual tree species.

In fact, because the life of the planet remains mostly unexplored at the species and infraspecies levels, systematists do not know the species diversity of the total world fauna and flora to the nearest order of magnitude. It is easily possible that the true number of species is closer to 10^8 than 10^7. Relatively little effort has been expended on nematodes, mites, or fungi, each highly diverse and containing undescribed species that could easily range into the hundreds of thousands or millions. Bacteria, with only about 4000 described species, remain a terra vitae incognita because of the astonishingly small amount of research devoted to their diversity, as opposed to the genetics and molecular biology of select species.

Hyperdiversity

Certain taxa are hyperdiverse, that is, they contain more species, genera, or higher ranked groups within them than expected by a null model of random assortment (*11*). Examples include arthropods among animal phyla, insects among arthropods, rodents among mammalian orders, orchids among monocotyledonous plant families, *Sciurus* among the genera of Sciuridae (squirrels), and so forth. It can be expected in a Darwinian world, where chance and opportunism prevail, that production of great diversity depends to substantial degree on special adaptations allowing penetration of multiple niches, such that each hyperdiverse group has its own magic key. For example, the ants appear to have expanded by virtue of fungistatic secretions, series-parallel work operations, and a highly altruistic worker caste (*12*). But recent research has also begun to identify properties possessed by many groups: small size, permitting fine niche subdivision (*7, 13, 14*); phytophagy and parasitism with specialization on hosts (*15*); specialized life stages that allow species to occupy multiple niches; entry into new geographic areas with subsequent adaptive radiation and preemption; and greater dispersal ability, promoting the colonization of empty areas. Southwood has neatly summarized the likely causes of the extreme hyperdiversity of insects as "size, metamorphism, and wings" (*13*).

Hyperdiversity also occurs in certain habitats and geographical areas. The strongest trend worldwide is the latitudinal diversity gradient, with group after group reaching its maximum richness in the tropics and most particularly in the tropical rain forests and coral reefs. (Exceptions include conifers, salamanders, and aphids.) The hyperdiversity of continental rain forests is legendary. Gentry found about 300 tree species in single-hectare plots in Peru (*16*), to be compared with 700 native tree species in all of North America. A single tree in the same area yielded 43 species of ants in 26 genera, about equal to the ant fauna of the entire British isles (*17*). Explaining the latitudinal diversity gradient has proven an intractable problem. But clues exist which when pieced together suggest the possibility of a general explanation, involving climatic stability and extreme biological specialization and niche division (*18*).

Natural Extinction

One of the qualities reducing diversity in particular groups is extinction proneness, which renders populations vulnerable to environmental change and reduces taxonomic groups to one or a very few threatened species. A threatened or endangered species (the two grades commonly employed by conservationists) is one with a high probability of extinction during the next few years or decades. The principal demographic properties contributing to the status are a low maximum breeding population size and a high coefficient of variation in that size (*19*). When the breeding size drops to a hundred or less, the likelihood of extinction is enhanced still further by inbreeding depression (*20*).

The overall natural extinction rate (at times other than mass extinction episodes) estimated from fossil data to the nearest order of magnitude is 10^{-7} species per species year (*21*). This estimate refers to true extinction, from the origin of a species to the extinction of that species and any species descended from it (altogether, called the clade) and excludes "pseudoextinction," the evolution of one species into another. Wide variation exists among major taxonomic groups in the longevity of clades. Mesozoic ammonoid and Silurian graptolite clades lasted only 1 million to 2 million years, whereas most other Paleozoic and Mesozoic invertebrate clades lasted closer to 10 million years (*21*). In general, planktonic and sessile marine animals, including corals and brachiopods, have had higher extinction rates than mobile benthic animals such as gastropods and bivalves (*22*). Using anatomical evidence from fossils and comparisons with related living species, paleobiologists have begun to infer the determinants of clade longevity by relating the adaptations of the organisms to maximum population size, population fluctuation, and dispersal ability (*23*).

Human-Caused Extinction

Biodiversity reduction is accelerating today largely through the destruction of natural habitats (*1*). Because of the latitudinal diversity gradient, the greatest loss occurs in tropical moist forests (rain forests) and coral reefs. The rate of loss of rain forests, down to approximately 55% of their original cover, was in 1989 almost double that in 1979. Roughly 1.8% of the remaining forests are disappearing per year (*24*). By the most conservative estimate from island biogeographic data, 0.2 to 0.3% of all species in the forests are extinguished or doomed each year (*25*). If two million species are confined to the forests, surely also a very conservative estimate, then extinction due to tropical deforestation alone must be responsible for the loss of at least 4000 species annually.

But there may well be 20 million or more species in the forests, raising the loss tenfold. Also, many species are very local and subject to immediate extinction from the clearing of a single habitat isolate, such as a mountain ridge or woodland patch (*26*). The absolute extinction rate thus may well be two to three orders of magnitude greater than the area-based estimates given above. If current rates of clearing are continued, one-quarter or more of the species of organisms on Earth could be eliminated within 50 years—and even that pessimistic estimate might be conservative (*25*). Moreover, for the first time in geological history, plants are being extinguished in large numbers (*27*).

Another data set illuminating the urgency of dealing with the extinction problem measures the human impact on global net primary productivity (NPP) (*28*); global NPP is roughly the total food supply of all animals and decomposers. Almost 40% of all NPP generated on land is now directly used, coopted, or forgone because of the activities of just one animal species—*Homo sapiens*.

Since the overwhelming majority (possibly more than 90%) of species now exists on land, the 40% human appropriation there alone shows why there is an extinction crisis. Furthermore, the human population is projected to double in the next half-century or so—to more than 10 billion people. Most ominous of all, the widely admired Brundtland Report speaks of a five- to tenfold increase in global economic activity needed during that period to meet the demands and aspirations of that exploding population (*29*). If anything remotely resembling that population-economic growth scenario is played out, with an acceleration of habitat destruction, most of the world's biodiversity seems destined to disappear.

Why Should We Care?

The loss of biodiversity should be of concern to everyone for three basic reasons (*1, 30*). The first is ethical and esthetic. Because *Homo sapiens* is the dominant species on Earth, we and many others think that people have an absolute moral responsibility to protect what are our only known living companions in the universe. Human responsibility in this respect is deep, beyond measure, beyond conventional science for the moment, but urgent nonetheless. The popularity of ecotourism, bird-watching, wildlife films, pet-keeping, and gardening attest that human beings gain great esthetic rewards from those companions (and generate substantial economic activity in the process).

The second reason is that humanity has already obtained enormous direct economic benefits from biodiversity in the form of foods, medicines, and industrial products, and has the potential for gaining many more. Wheat, rice, and corn (maize) were unimpressive wild grasses before they were "borrowed" from the library and developed by selective breeding into the productive crops that have become the feeding base of humanity. All other crops, as well as domestic animals, have their origins in the genetic library, as do many medicines and various industrial products, including a wide variety of timbers (*1, 30*). Throughout the world almost a quarter of all medical prescriptions are either for chemical compounds from plants or microorganisms, or for synthetic versions or derivatives of them (*31*). One plant compound, quinine, is still a mainstay of humanity's defense against its most important disease, malaria.

Biodiversity is a precious "genetic library" maintained by natural ecosystems. But the potential of the library to supply such benefits has barely been tapped. Only a tiny portion of plant species has been screened for possible value as providers of medicines (*31*), and although human beings have used about 7000 plant species for food, at least several times that number are reported to have edible parts (*1*).

The third reason, perhaps the most poorly evaluated to date, is the array of essential services provided by natural ecosystems, of which diverse species are the key working parts. Ecosystem services include maintenance of the gaseous composition of the atmosphere, preventing changes in the mix of gases from being too rapid for the biota to adjust. In Earth's early history, photosynthesizing organisms in the seas gradually made Earth's atmosphere rich in oxygen. Until there was enough oxygen for an ozone shield to form, the land surface was bathed in ultraviolet-B radiation. Up to some 450 million years ago life was confined to the seas. Only with the protection of the ozone shield were plants, arthropods, and amphibians able to colonize the land.

Significant alteration of the atmosphere has signaled the arrival over the past few decades of *Homo sapiens* as a global force, one capable of destroying most of biodiversity. As a result of human activities (*32*), the ozone shield has thinned by as much as 5% over Europe and North America (*33*), and there is some evidence that the surface intensity of ultraviolet-B radiation has increased there (*34*). Each spring the shield is now reduced over the Antarctic by approximately 50%. The global impact of the human economy is even more evident in the prospect of climatic change in response to increasing concentrations of greenhouse gases (*35*).

The organisms in natural ecosystems influence the climate in ways other than the role they play in regulating atmospheric gases. The vast rain forests of Amazonia to a large degree create the moist conditions that are required for their own survival by recycling rainfall. But as the forest shrinks under human assault, many biologists speculate that there will be a critical threshold beyond which the remaining forest will no longer be able to maintain the climate necessary for its own persistence (*36*). Deforestation and the subsequent drying of the climate could have serious regional effects in Brazil outside of Amazonia, conceivably reducing rainfall in important agricultural areas to the south. There also appear to be regional effects on climate when semi-arid regions are desertified (*37*), but their extent remains unknown.

The generation and maintenance of soils is another crucial service supplied most efficiently by natural ecosystems. Soils are much more than fragmented rock; they are themselves complex ecosystems with a rich biota (*38*). The elements of biodiversity in soil ecosystems are crucial to their fertility—to their ability to support crops and forests.

Many green plants enter into intimate relationships with mycorrhizal fungi in the soil. The plants nourish the fungi, which in turn transfer essential nutrients into the roots of the plant. In some forests where trees appear to be the dominant organisms, the existence of the trees is dependent upon the functioning of these fungi. On farms, other microorganisms play similar critical roles in transferring nutrients to crops such as spring wheat.

Organisms are very much involved in the production of soils, which starts with the weathering of the underlying rock. Plant roots can fracture rocks and thus help generate particles that are a major physical component of soils; plants and animals also contribute CO_2 and organic acids that contribute to the weathering of parent rock. More importantly, many species of small organisms, especially bacteria, decompose organic matter (shed leaves, animal droppings, dead organisms, and so on), releasing carbon dioxide and water into the soil and leaving a residue of humus, or tiny organic particles. These are resistant to further decomposition, help maintain soil texture and retain water, and play a critical role in soil chemistry, permitting the retention of nutrients essential for plant growth.

Soil ecosystems themselves are the main providers on land of two more essential ecosystem services: disposal of wastes and cycling of nutrients. Decomposers break wastes down into nutrients that are essential to the growth of green plants. In some cases, the nutrients are taken up more or less directly by plants near where the decomposers did their work. In others, the products of decomposition circulate through vast biogeochemical cycles before being reincorporated into living plants.

Another critical service provided by natural ecosystems is the control of the vast majority of species that can attack crops or domestic animals. Most of those potential pests are herbivorous insects, and the control is provided primarily by numerous species of predacious and parasitic insects that naturally feed upon them.

While natural ecosystems are providing crop plants with stable climates, water, soils, and nutrients, and protecting them from pests, they also often pollinate them. Although honeybees, essentially domesticated organisms, pollinate many crops, numerous other crops depend on the services of pollinators from natural ecosystems. One such crop is alfalfa, which is most efficiently pollinated in cooler areas by wild bees.

The biodiversity in natural ecosystems also supplies people with food directly—most notably with a critical portion of their dietary protein from fishes and other marine animals. This service is provided by oceanic ecosystems in conjunction with coastal wetland habitats that serve as crucial nurseries for marine life.

The ecosystem services in which biodiversity plays the critical role are provided on such a grand scale and in a manner so intricate that there is usually no real possibility of substituting for them, even in cases where scientists have the requisite knowledge. In fact, one could conclude that virtually all human attempts at large-scale inorganic substitution for ecosystem services are ultimately unsuccessful, whether it be introductions of synthetic pesticides for natural pest control, inorganic fertilizer for natural soil maintenance, chlorination for natural water purification, dams for flood and drought control, or air-conditioning of overheated environments. Generally, the substitutes require a large energy subsidy, thereby adding to humanity's general impact on the environment, and are not completely satisfactory in even the short run (*39*).

It is important to note that in supplying ecosystem services the species and genic diversity of natural systems is critical. One might assume that one grass or tree species can function as well as any other in helping control the hydrologic cycle in a watershed, or that one predator will be as good as another in controlling a potential pest. But, of course, organisms are generally highly adapted to specific physical and biotic environments—and organic substitutions, like inorganic ones, are likely to prove unsatisfactory.

In sum, much of biodiversity and the quality of ecosystem services generated by it will be lost if the epidemic of extinctions now under way is allowed to continue unabated.

Public Policy

Many steps can be taken to preserve biodiversity, if the political will is generated. Perhaps the first step, which would be seen as especially extreme by Americans, would be to cease "developing" any more relatively undisturbed land. Every new shopping center built in the California chaparral, every hectare of tropical forest cut and burned, every swamp converted into a rice paddy or shrimp farm means less biodiversity.

In rich countries, stopping the more destructive forms of "development" is relatively simple in principle. Age structures are such that population shrinkage in most rich nations could be achieved with little effort (a few are already in that desirable mode). When new facilities are needed, they should replace deteriorating old ones. Forestry should be placed on a sustainable basis with careful attention to the conservation of precious reserves of old growth. And much more scientific effort and public support should go into biodiversity studies, including the cataloging of the genetic library and national biological inventories (*1, 31*).

In poor nations, the task is both more urgent and vastly more difficult. It cannot be accomplished immediately, and will not be accomplished at all without massive assistance from the rich. For instance, stopping the expansion of cropland and pasture into virgin areas cannot be accomplished unless birth rates can be dramatically lowered and the development of sustainable high-yield agricultural systems is backed by land reform and a sound agricultural infrastructure and economy. In many cases, new social and economic systems must be developed in which preservation of biodiversity and its sustainable exploitation go hand in hand. The social, political, economic, and scientific barriers to achieving the goal are so formidable that nothing less than the kind of commitments so recently invested in the Cold War could possibly suffice to accomplish it. And we are 45 years late in starting.

But ending direct human incursions into remaining relatively undisturbed habitats would be only a start. Simultaneously, global cooperative efforts to reduce anthropogenic impacts on ecosystems, such as those directed at a reduction of emissions of greenhouse gases and ozone-destroying compounds, must be greatly enhanced. They are much more likely to be successful if population growth can be halted and the cessation of forest destruction can be achieved.

Finally, because humanity already occupies so much of Earth's surface, substantial effort should be directed at making areas already used by people more hospitable to other organisms. Those efforts can range from the substitution of game ranching for cattle and sheep ranching in many areas to the substitution of native vegetation for European-style lawns in desert cities.

If there is to be any chance of abating the loss of biodiversity, action must be taken immediately. The essential tactics of conservation are being developed within conservation biology, as a subdiscipline of biodiversity studies. The indispensable strategy for saving our fellow living creatures and ourselves in the long run, is, as the evidence compellingly shows, to reduce the scale of human activities. The task of accomplishing this goal will involve a cooperative worldwide effort unprecedented in history. Unless humanity can move determinedly in that direction, all of the efforts now going into in situ conservation will eventually lead nowhere, and our descendents' future will be at risk.

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Research Article

Convergence of Ets- and Notch-Related Structural Motifs in a Heteromeric DNA Binding Complex

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Analysis of the heteromeric DNA binding protein GABP has revealed the interaction of two distinct peptide sequence motifs normally associated with proteins located in different cellular compartments. The α subunit of GABP contains an 85–amino acid segment related to the Ets family of DNA binding proteins. The ETS domain of GABPα facilitates weak binding to DNA and, together with an adjacent segment of 37 amino acids, mediates stable interaction with GABPβ. The β subunit of GABP contains four imperfect repeats of a sequence present in several transmembrane proteins including the product of the *Notch* gene of *Drosophila melanogaster*. These amino-terminal repeats of GABPβ mediate stable interaction with GABPα and, when complexed with GABPα, directly contact DNA. These observations provide evidence for a distinct biochemical role for the 33–amino acid repeats, and suggest that they may serve as a module for the generation of specific dimerization interfaces.

SINCE THE INITIAL RECOGNITION OF A COMMON PROTEIN sequence motif in the *SWI6* gene product of *Saccharomyces cerevisiae* and the *Notch* gene product of *Drosophila melanogaster* (*1*), similar sequences have been identified in different biologically interesting proteins. The motif, variously termed the cdc10/SWI6 or ankyrin repeat, consists of a 33–amino acid sequence often present in tandem arrays. This motif has been observed in the products of the *Notch, lin-12*, and *glp-1* genes, putative transmembrane proteins of *Drosophila melanogaster* and *Caenorhabditis elegans* that transmit signals critical for specification of cell fate (*2*); the product of *fem-1*, a *Caenorhabditis elegans* gene that regulates sex determination (*3*); cdc10, SWI4, SWI6, yeast proteins involved in cell cycle control (*1, 4*); ankyrin, a multifunctional protein of the red blood cell cytoskeleton (*5*); the product of *bcl-3*, a human gene located near a translocation breakpoint associated with some leukemias (*6*); the 105-kD precursor to the active 50-kD subunit of NFκB/KBF1 (*7*); and IκB, a regulatory subunit of NFκB that inhibits DNA binding and has been implicated in cytoplasmic sequestration (*8*). Despite the widespread occurrence of the 33–amino acid motif, its functional role has heretofore remained obscure.

Our interest in the 33–amino acid repeat arose from studies of GA binding protein (GABP), a multisubunit DNA binding protein purified from rat liver nuclei (*9*). GABP was originally identified as a factor that binds to a cis-regulatory element required for VP16-mediated activation of herpes simplex virus (HSV) immediate early genes (*10*). Biochemical and molecular biological experiments have shown that GABP is composed of two distinct polypeptides, both of which are required for avid interaction with DNA (*9, 11*). The amino acid sequence of the GABPα subunit exhibits similarity to the Ets family of nuclear proteins, whereas that of GABPβ contains a tandem series of 33–amino acid, cdc10/SWI6 repeats (*11*). We now demonstrate that it is these two distinct protein sequence motifs that form the heteromeric interface between GABPα and GABPβ.

We view the 33–amino acid repeat as a versatile module for the

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Preserving Biodiversity

The preservation of species diversity is a problem that must today be confronted by one species, *Homo sapiens*. That one species has become so efficient at reproducing itself and dominating all other forms of life that it is in the act of endangering all species, including itself. Thus, in the long, evolutionary battle, *Homo sapiens* has prevailed, by using its brains, but will win only if it can now use the same brains to limit its victory and ensure its own survival.

As Ehrlich and Wilson point out in an article in this issue, there may now be as many as 100 million species, but if current rates of development continue, one quarter of them could be eliminated within 50 years. The human population is projected to double in the next half century, with a possible five- to tenfold increase in global economic activity projected to meet the demands of the growing population. Such uncontrolled growth would threaten all the species of the earth.

For this issue of *Science* we also invited a number of scientists interested in the area of biodiversity to define the crisis and suggest solutions. No consensus is reached, but a number of steps in the right direction are mentioned, all of which require political courage. Jablonski puts the problem in paleontological perspective. In the past, species extinction and recovery occurred over relatively long periods. Nine thousand years, the estimated time of the extinction of large mammals in the Pleistocene, is a short period in terms of evolutionary time, which is measured in millions of years, but an extremely long period in terms of political time, which is usually measured in 4 ± 2 years. The dilemma for the saving of species is therefore that politicians, listening to the anguish of farmers, homeowners, and even scientists, must put off present crises in order to help future constituents who would at best vote for their great-grandchildren. Moreover, there is no obvious solution to which all the biodiversity advocates can point.

Yet a pattern does emerge from the points of view expressed in this issue. Soulé neatly divides the subject into five areas of knowledge about biological diversity, six major classes of human interference, seven areas of biotic degradation, and an eightfold road to possible solutions. Morowitz takes the side that not all species can be saved. He argues that the uniqueness of a particular species should be a component of priority setting and that emphasis should be shifted to priority for habitat preservation. Erwin places priority on evolutionarily dynamic lineages that will create future biodiversity. Charles Mann interviews paleontologists and others who question the pervasiveness of the extinction data.

What emerges from these papers, which provide an excellent starting point for focusing on possible solutions, is that the diversity of species is worth preserving because it represents a wealth of knowledge that cannot be replaced. Moreover, today's extinctions are unlike those in previous eras, in which long periods of recovery could follow extinctions. The present situation is an inexorably irreversible one in which human overpopulation will destroy most species unless we plan for protection immediately.

Accepting that the goal is worthwhile requires that more energy be devoted to planning and priorities and less to emotionalism and indignation. It seems obvious that an attempt to save every species will irritate loggers, dam-builders, astronomers, and eventually all others, and is an impossible chore. Numbers alone are not the answer. Millions of new beetles do not compensate for the loss of lions, tigers, and elephants. As these scientists point out, however, a multi-pronged approach—expanding the list of protected areas, judiciously choosing certain species for preservation, providing artificial environments such as zoos, botanical gardens, germ plasm storage, seed banks, and so on—are parts of a program that is feasible.

Once agreement is reached on the measures that must be taken, the political and moral problems must be faced. Some of the most obvious solutions involve preserving wild natural areas in developing countries, where the land is cheap, but the human need for it is desperate. In the developed countries, the humans are better off, but the land has become very valuable, and important habitats may border on densely populated areas.

We may need to select politicians whose time scale is in Pleistocene epochs rather than terms of elective office. Southwood has explained the hyperdiversity of insects as based on "size, metamorphism, and wings." *Homo sapiens* even without wings has expanded more effectively than any other species because of its brains. It is time we use them for the benefit of posterity.—DANIEL E. KOSHLAND, JR.

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Habitat fragmentation: island v landscape perspectives on bird conservation

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Fragments of habitat are often viewed as islands and are managed as such; however, habitat fragmentation includes a wide range of spatial patterns of environments that may occur on many spatial scales. Fragments exist in a complex landscape mosaic, and dynamics within a fragment are affected by external factors that vary as the mosaic structure changes. The simple analogy of fragments to islands, therefore, is unsatisfactory. Understanding how birds respond to these complexities of fragmentation requires mechanistic studies focused on habitat selection and movement behaviour. Conservation efforts must be based on viewing fragmentation as a range of conditions that occurs in a landscape mosaic, and management should be directed toward the mosaics rather than focusing solely on reserves.

The destruction of natural and semi-natural habitats is proceeding at an alarming rate in many parts of the world. Broad expanses of forest have been reduced to isolated fragments, and natural prairies exist only as tiny relics. In the wheatbelt region of western Australia, for example, 93% of the native vegetation has been cleared since European settlement, much of it within the last 50 years (Saunders *et al.* 1993). Concurrently, 41 bird species (nearly 30% of the avifauna) have decreased in range or abundance (Hobbs *et al.* 1992). The effects of habitat fragmentation are so pervasive that it has been called "the principal threat to most species in the temperate zone" (Wilcove *et al.* 1986) and "the single greatest threat to biological diversity" (Noss 1991).

Conservation biologists generally believe that habitat fragmentation has a variety of negative consequences (Merriam 1988, Bennett 1990, Saunders *et al.* 1991, Haila *et al.* 1993). In addition to an overall loss of habitat, the size of habitat remnants is reduced, blocks of habitat become widely separated and the proportion of habitat that is close to patch boundaries increases and the edges become more abrupt. As a result of the area effects, population sizes are reduced, leading to the disappearance of some species from small fragments and an increased sensitivity of the remaining populations to chance events. Because of fragment isolation, recolonization following local extinctions may be slowed. Species diversity is reduced and community composition is altered because some species, such as large predators or sedentary specialists, are especially sensitive to these effects (Temple 1991, Bierregaard *et al.* 1992). As a consequence of edge effects, population and community dynamics within a patch may be dominated by external factors such as predation, parasitism or physical disturbances. These changes may be accompanied by less obvious, indirect effects. If fragmentation affects the distribution and abundance of insects, for example (e.g. Roland 1993), the resource base of insectivorous birds may be altered. The loss of large predators may be followed by an increase in the abundance of herbivores that browse the vegetation, altering the habitat structure available to birds (Angelstam 1992).

These consequences of fragmentation are rapidly becoming established as dogma in conservation biology. Empirical evidence of fragmentation effects, however, is meagre, and much of it comes from studies of temperate forest patches in agricultural settings that may not apply to other situations (Hunter 1991). Our perception of fragmentation effects seems to have been based less on observations and data than on theoretical expectations, particularly those associated with island biogeography theory (MacArthur & Wilson 1967, Wilson & Willis 1975). Although the usefulness of this theoretical framework has been questioned (e.g. Gilbert 1980, Zimmerman & Bierregaard 1986, Merriam 1988, Wiens 1989a, 1990, Soberón 1992, Haila *et al.* 1993), it has dominated much of our thinking about fragmentation and has dictated which variables should be measured (e.g. area, isolation, number of species present). As a result, some important aspects of fragmentation have been obscured or ignored.

Perhaps as a result of the combined inadequacies of the empirical evidence and the conceptual framework, our present knowledge of how fragmentation affects birds remains uncertain. In the remainder of this paper, I discuss four features that are critical to understanding the reality of fragmentation and its effects. I conclude by commenting on how this reality may affect conservation practices.

FRAGMENTATION IS NOT A UNITARY PHENOMENON

"Fragmentation" can refer either to the spatial *pattern* of patchiness of a habitat or to the *process* that produces such

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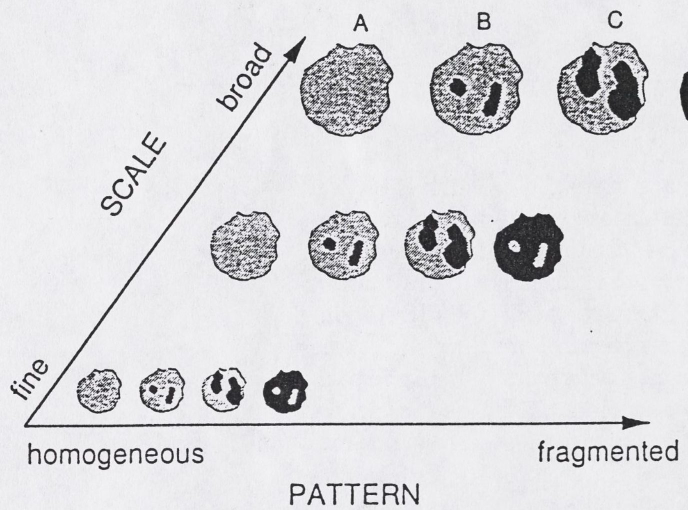

Figure 1. Variations in habitat fragmentation. On the abscissa are displayed four stages on a continuous gradient of habitat change, ranging from homogeneous (A) to highly fragmented (D). The ordinate indices indicate spatial scale on a continuous gradient from fine to broad (in a relative sense). The full range of possible states of habitat fragmentation may be expressed at any particular scale, which may then be a subset of a similar or different spatial pattern at a broader scale. Because species differ in the scales on which they perceive or respond to environmental patterns, generalizations among species are difficult. The variation in spatial patterning and the range of scales over which it is expressed preclude simple categorizations of habitats as "fragmented" or "unfragmented". "Fragmentation" is best viewed as encompassing the full spectra of patterns and scales.

a pattern. The process may be defined as a disruption of habitat continuity (Lord & Norton 1990, Harris & Silva-Lopez 1992). Such disturbances may produce a variety of patterns, ranging from small breaks in an otherwise homogeneous habitat (e.g. treefall gaps in forests, patches of woody vegetation in a prairie) to widely scattered units of remnant habitat in a transformed matrix (e.g. parks in a city) (Fig. 1). Although we normally think only of the latter as a fragmented habitat, the various stages on the abscissa of Figure 1 grade into one another and represent variations on the theme of breakage of habitat continuity. In the remainder of this paper, I use "fragmentation" or "fragmented" to refer to conditions B–D of Figure 1.

Often, our view of fragmentation also carries a habitat bias. In Figure 1, patterns B and D are essentially mirror images of one another; which we choose to term fragmented depends entirely on what we view as "habitat" and what as "matrix". Different perspectives, however, may yield different results. For example, Rudnicky and Hunter (1993) found that patterns of avian species richness and species' incidence functions in small fragments of clearcut habitat immersed in otherwise continuous forest differed from those normally associated with fragments of forest in a clearcut or agricultural landscape.

Some of the difficulty in understanding fragmentation effects may result from uncertainty in defining what is fragmented and what is not. If one equates fragments with islands, the problem is simplified, for then fragments are by definition isolated from other blocks of similar habitat. Variations in the extent of fragmentation can be measured by fragment size and the degree of isolation. This view is reinforced by applications of percolation theory in landscape ecology (Gardner *et al.* 1991), which suggest that as the amount of habitat in an area is reduced there may be an abrupt threshold at which the diffusion of individuals among patches is sharply reduced. The gradient depicted in Figure 1, however, is continuous, and it would seem better to consider it so rather than to partition it arbitrarily into "fragmented' and "unfragmented" categories solely on the basis of patch isolation.

Scale dependence in habitat patterns, and in how different organisms respond to them, may also contribute to our uncertainty about fragmentation effects. Habitat management is usually practised at a scale relevant to humans, from a few to hundreds of hectares. The appropriate ecological scale, however, varies with both the organisms and the questions of interest (Wiens 1989b, Haila 1991, Levin 1992). These differences in scaling affect our thinking about fragmentation in several ways. An area that is broken into 1-ha blocks of forest and clearcut, for example, may represent fragments of suitable *v* unsuitable habitat to an individual with a small home range, such as a North American *Dendroica* warbler, but be perceived as a fine-grained mixture of small patches by an individual with a large home range, such as a forest *Accipiter* hawk (Hunter 1990). Conversely, a given pattern of patchiness may be expressed over a range of spatial scales (Fig. 1), and individuals of the same or different species may respond differently at different scales (Kremsater & Bunnell 1992). The effects of the scale of fragmentation will also differ depending on whether one's focus is on individuals or on populations (or metapopulations) (Lord & Norton 1990, Van Horne 1991). Individual Capercaillie *Tetrao urogallus* cocks require 20–50 ha of old forest for a territory at a lek, whereas a lek itself may require 200–500 ha dominated by old forest. A local breeding group, however, may use *c.* 10,000 ha of forest (Rolstad & Wegge 1987, Angelstam 1992). A given degree of fragmentation may mean something quite different at these different levels.

Spotted Owls *Strix occidentalis* provide a good example of how scaling functions may affect management plans. Annual home ranges of individual owls may vary from as little as 500–600 ha to over 5000 ha in different regions (Thomas *et al.* 1990; see also Carey *et al.* 1992). Individuals in different regions, therefore, may perceive habitat patterns on different scales. Because of these differences in home-range size and differences in the degree of habitat fragmentation and loss in different regions, the area that must be preserved to support a breeding pair of owls differs regionally as well. For these reasons, conservation plans have been based on managing the habitat needed to support a certain number of pairs rather than setting aside a fixed area of habitat.

Nonlinearity also contributes to uncertainty about fragmentation effects. Although the response of communities to fragmentation (i.e. island area) is often depicted as a monotonic species–area (S/A) relationship, this approach seems uninformative. "Area" includes many factors other than patch area *per se*, and "species" does not distinguish among species that may respond in quite different ways. In fact, the response of most species to changes in fragment size is usually not linear. Incidence functions, which chart the frequency of occurrence of a species among fragments as a function of fragment size (Diamond 1975, Opdam *et al.* 1985), usually show a sharp break: species are present in virtually all patches above a certain size and occur much less frequently in smaller patches. Incidence functions differ among species, so the effects of an incremental amount of habitat change on the gradient in Figure 1 may differ at different points along the gradient. Successful habitat management depends on knowing how the community of species present in an area responds to habitat changes along this gradient. Consideration of only the extremely fragmented end of the spectrum will obscure these dynamics and fail to provide appropriate guidance for restoration efforts.

FRAGMENTS ARE NOT ISLANDS

Unlike real islands, habitat fragments are rarely surrounded by an ecologically neutral or inhospitable environment. Fragments are open to influences from the surrounding landscape, and these effects may be more important than processes occurring within a fragment (Wiens *et al.* 1985, Hansen & di Castri 1992, Hobbs 1993). In the Arizona desert, for example, bird species characteristic of riparian woodland fragments may contribute as much as a third of the individuals found in nearby dry streambeds and perhaps a sixth of the total density in adjacent desert uplands (Szaro & Jakle 1985). The influence of the woodland decreases with increasing distance from its edge, but the decrease is much more rapid in the upland than in the streambed habitats.

What goes on within a habitat patch, then, may be affected by the boundary with adjacent habitats. The effects of patch edges on bird populations and communities, however, are not always the same. In Swedish clearfelled areas surrounded by forest, for example, species richness was lower near the patch edge (Hansson 1983), whereas no such edge effect was apparent in clearfelled areas in northeastern U.S.A. (Rudnicky & Hunter 1993). In some situations, the steepness of the habitat change across a patch boundary may have important effects. Thus, small breaks created by clearing next to fragments of tropical forest may act as a strong barrier to movement by many understory birds, but as vegetation in the clearings regenerates, the patch boundary becomes less sharp and movement of some of these species is enhanced (Bierregaard *et al.* 1992).

Predation rates are often greater near the forest/farmland edge than in the forest interior (Gates & Gysel 1978, Wilcove 1985, Temple & Cary 1988, Andrén & Angelstam 1988, Andrén 1992, Angelstam 1992), but the same may not be true for edges between forests and clearcuts (M. L. Hunter, pers. comm.) or in fragments of chaparral habitat (Langen *et al.* 1991). Wilcove's (1985) experimental studies demonstrated that predation rates in small forest fragments varied as a function of fragment size, but predation was also generally greater in fragments located in a suburban landscape than in a rural setting. Yahner & DeLong (1992) found predation rates on experimental nests in forest/clearcut mosaics similar to those in forest/farmland mosaics, although the rates they reported were considerably lower than those documented in another forest/farmland mosaic in the same region (Yahner & Morrell 1991). Nest predation may often be a result of incidental encounter of nests by predators (Angelstam 1986, Vickery *et al.* 1992), and these variations in predation rates with respect to patch edges, fragment types or nearby habitats may stem from differences in the densities (and types) of predators present. Whether or not edges increase predation risk may depend on whether predators are naturally more abundant in an adjoining habitat or are attracted to the habitat ecotone. Because of these variations, the notion that fragment edges might function as an "ecological trap" (by attracting birds to establish territories on edges where food supplies may be greater but nest predation is increased [Gates & Gysel 1978]) may not apply generally, although it is nonetheless important to identify those situations where it may be a problem.

These examples indicate that what goes on within a fragment is sensitive to the broader, landscape context. Landscapes have a variety of features (Wiens *et al.* 1993), but much of the attention in conservation debates has centered on the importance of corridors linking otherwise isolated habitat fragments (Bennett 1990, Saunders & Hobbs 1991, Hobbs 1992, Merriam & Saunders 1993). By facilitating movement of individuals, corridors are widely thought to reduce the vulnerability of small subpopulations to chance extinction and to enhance the recolonization of empty habitat patches, thereby fostering metapopulation persistence (Lefkovitch & Fahrig 1985, Merriam 1991, Soulé & Gilpin 1991). Corridors (or linear fragments) may also be important habitats in their own right; in Britain and Europe, for example, hedgerows may contribute significantly to the species richness of an area (Osborne 1984, Van Dorp & Opdam 1987).

The evidence that species do depend on corridors for their movements or that corridors have clear conservation value, however, is limited and equivocal (Hobbs 1992). Some species clearly do use habitat corridors to move between areas. In North America, for example, Blue Jays *Cyanocitta cristata* make extensive use of fencerow corridors as they move from forests to winter food caches (Johnson & Adkisson 1985). In Western Australia, Carnaby's Cockatoos *Calyptorhynchus funereus* use roadside vegetation as pathways for foraging movements within their large home ranges (Saunders 1990), and they have disappeared from areas in which the food sources are widely isolated. Western Yellow Robins *Eopsaltria griseogularis*, which are dependent on remnant forest vegetation, move along well-vegetated links between larger wooded fragments (Saunders 1989). In contrast, Singing Honeyeaters *Lichenostomus virescens*, which are habitat generalists, readily fly across open agricultural areas with little vegetation (Merriam & Saunders 1993). Dispersing Spotted Owls apparently do not require corridors of the old-growth forest that is so important for breeding (Thomas *et al.* 1990).

Corridors may have a variety of negative as well as positive effects (Simberloff & Cox 1987, Hobbs 1992), and their value in avian conservation and management may be overrated. Rather than limiting attention to movement through corridors of habitat similar to that in the fragments of interest, it may be more appropriate to focus on landscape *connectivity*, the probability of movement among all types of habitat patches in a landscape (Merriam 1991, Taylor *et al.* 1993). Thus, animals may be able to move through a variety of habitats in a mosaic but do so at different rates depending on the "resistance" of the habitats to movement and the overall configuration or "networking" of the landscape.

FRAGMENTATION IS A DYNAMIC PROCESS

Landscapes, and the populations they contain, are not stable through time. Landscapes change as a consequence of small- and large-scale disturbances, some natural (e.g. lightning fires, insect outbreaks), others anthropogenic (e.g. forest cutting, abandonment of agricultural fields). Fragments appear and, with vegetational regeneration, may become less distinct and eventually disappear. Such temporal dynamics of landscape patterns may have profound effects on population persistence (Fahrig 1992).

There are also important temporal dynamics to the responses of populations to habitat fragmentation. Because of site fidelity, some individuals may not respond immediately to habitat changes (Wiens & Rotenberry 1985, Temple & Wiens 1989). This will delay the appearance of fragmentation effects. By replacing losses of territorial individuals, floaters in a population can have a similar effect. Other species may respond to the loss of habitat by moving immediately into the remaining fragments, temporarily increasing species richness and densities in the fragments (Bierregaard *et al.* 1992). Social attraction among individuals (e.g. breeding coloniality) may also alter the pattern of distribution of individuals among fragments and create time lags in responses to landscape change (Smith & Peacock 1990, Weddell 1991). These processes all reduce the likelihood that the local distribution of individuals among patches in a mosaic will reach an equilibrium before the landscape undergoes further change.

The attainment of a local equilibrium between population distribution and fragmentation patterns may also be thwarted by environmental variations that occur over much broader spatial scales. In Australia, for example, Magpie Geese *Anseranas semipalmata* breed in naturally fragmented wetlands. Breeding populations in a particular location fluctuate dramatically, however, apparently in response to both local and broad-scale rainfall variations (Woinarski *et al.* 1992). In Australia, the great mobility of many organisms may be an adaptation to such broad-scale climatic variations (Wiens 1991). The responses of such populations to temporal changes in mosaic patterns are likely to be quite different from those of more sedentary species. Both the scales on which organisms respond to habitat patchiness and the scales in time and space on which mosaic patterns vary are important in determining how a species may respond to fragmentation.

UNDERSTANDING FRAGMENTATION REQUIRES KNOWLEDGE OF MECHANISMS

It is clear from the preceding examples that how individuals perceive patchiness and how they move among fragments influence how they are affected by fragmentation. It is therefore appropriate to practise some judicious reductionism and focus on the mechanisms that may determine how individuals respond to a mosaic. It is not likely that such a focus will provide a complete understanding of fragmentation effects because the habitat distribution of populations and communities may also be influenced by higher level constraints such as density dependence (Stenseth & Hansson 1981) or the regional and biogeographic dynamics of species distributions (Ricklefs & Schluter 1994). Still, some attention to individual-level mechanisms may enable us to move away from the largely phenomenological explanations that have characterized much of the previous work on fragmentation.

Two aspects of individual behaviour, habitat selection and movement, are central to understanding how organisms respond to the spatial texture of environments (Wiens *et al.* 1993). The habitat selection that is most relevant to fragmentation occurs when individuals encounter fragment boundaries and must choose between adjacent patches. If individuals readily cross corridor boundaries, for example, the "corridor" will not do much to enhance or direct movements. If individuals are repelled by edges, however, their dispersal may be reduced, especially if the corridor is narrow (Baur & Baur 1992). Although books have been written about habitat selection (e.g. Cody 1985), most research has dealt with the patterns of habitat association that result from the behaviour rather than with the process itself. Understanding the behavioural basis for patch choice is an urgent need.

Movement, and the resulting dispersal of individuals, is perhaps the key process determining how patch spacing affects populations (Fahrig & Paloheimo 1988, Opdam 1990, Hanski 1991). Because species differ in dispersal distances, a landscape that is fragmented into isolated patches for one species may be highly connected for another, and statements about fragment "isolation" therefore depend on the species being considered. Even within a species, however, dispersal distances may vary as a function of habitat. For example, median dispersal distances of young Nuthatches *Sitta europaea* were twice as great in a highly fragmented landscape in Belgium as in a more heavily forested area in Germany (J. Matthysen, pers. comm.).

Despite its importance, quantitative information on dispersal distances or on how individuals move through a mosaic environment is remarkably scarce (Opdam 1991, Harrison 1992). It seem evident, however, that relatively high mobility (and, to a lesser degree, generalized habitat selection) should counteract some of the effects of habitat fragmentation and that sedentary species should be much more vulnerable to changes in habitat configuration (Haila 1991, Bierregaard *et al.* 1992). One implication of these differences is that the island analogy may apply only to the most sedentary species.

IMPLICATIONS FOR CONSERVATION

Habitat fragmentation concerns conservation biologists because it results in habitat loss and threatens the persistence of species most closely associated with the habitat remnants. In seeking management solutions to these problems, much of the attention has focused on the creation of reserves to preserve threatened species or ecosystems. To a large degree, thinking about reserves is still guided by the "principles" derived from island biogeography theory (e.g. Wilson & Willis 1975); the intense SLOSS (single-large or several-small) debate is but a variation on this theme. Brussard *et al.* (1992), however, have argued forcefully that we must expand beyond this "reserve mentality" to prevent the public and politicians from concluding that, once reserves are established, the remaining lands can be used for any purpose.

Reserves are important, of course, but they are almost always inadequate to satisfy conservation goals completely. Neither fragments nor reserves are islands; they are strongly influenced by forces from other habitats in the landscape mosaic. Proper conservation therefore requires management of the mosaic itself rather than of selected habitat units within the mosaic (Harris 1984, Hobbs *et al.* 1993). Often, this may involve managing areas surrounding a reserve in a way that permits use (e.g. timber harvesting, grazing) within prescribed limits. One management plan for the Spotted Owl, for example, recommends that 50% of the forest area surrounding a conservation unit be in stands averaging 11 inches (28 cm) diameter at breast height and at least 40% canopy cover (the so-called 50–11–40 rule [Thomas *et al.* 1990]). Such management may need to be applied to private as well as public lands. Clearly, there are difficulties in implementing such an approach in a political system that promotes individual freedom and private enterprise, especially when it is coupled with economics driven by short-term profits.

Conservation and resource management should be based at least as much on science as on politics and economics. What does science have to offer those interested in managing fragmented landscapes? Insights may come from two sources: theory and empirical knowledge. It is clear that the contributions of island-based theory have been, at best, disappointing. The analogy of habitat fragments to islands does not provide a good model for understanding how changes in landscapes may affect populations (Simberloff & Abele 1984, Wiens 1990, Soberón 1992). Metapopulation theory may provide some valuable insights into conservation issues (Lande 1988, Opdam 1991), but it also relies largely on a patch–matrix conceptualization of spatial patterning. Basic metapopulation models assume that dynamics in different patches are independent and asynchronous, dispersal is limited and all patches are of the same size and are equally accessible to dispersers (Hanski 1991). Although these assumptions may be dealt with in some models (e.g. Verboom *et al.* 1993), it is still necessary to be certain that model assumptions are valid before metapopulation theory is applied to management situations. Landscape ecology might provide a better framework for thinking about fragmentation effects, but theory in this discipline is not yet well developed (Merriam 1988, Wiens in press). There are few useful, quantitative predictions to guide us in thinking about how the structure and dynamics of mosaics may influence populations, although developments in percolation theory (e.g. Gardner *et al.* 1991) and hierarchy theory (O'Neill *et al.* 1992) show some promise.

It has often been suggested that, given the failings of theory in conservation biology, we should rely more heavily on empirical, autecological information (Zimmerman & Bierregaard 1986, Wiens 1989a, Haila 1991, Hobbs 1992). Unfortunately, we have information on how populations respond to landscape change for very few species, and much of this information is derived from temperate species that are known to be sensitive to fragmentation, are declining in abundance or are common at patch edges. As a result, the empirical knowledge needed to develop a broad perspective on fragmentation effects does not yet exist. Experimental studies of fragmentation (e.g. Bierregaard *et al.* 1992, Robinson *et al.* 1992, Schmiegelow & Hannon 1993) are especially needed, but the logistical difficulties of conducting such experiments at broad spatial scales or with organisms as mobile as birds are formidable.

There has been a tendency in conservation biology, as in much of ecology, for thinking to be polarized between general theory and situation-specific empiricism. Clearly, we should not believe too much in general theory, but neither can we afford to undertake detailed autecological studies of every species in every situation in order to develop a firm scientific foundation for conservation and management. Instead, we should strive to (1) develop mosaic theory that has a specified and restricted domain of application, (2) target for study selected species that may serve as models for a larger suite of species that share ecological, life-history or distributional features (Wiens *et al.* 1993, Collins *et al.* 1993) and (3) integrate these two approaches. Above all, we must ensure that our conservation efforts rest upon strong science and that preliminary, academic concepts based on limited empirical information are not prematurely turned into management principles.

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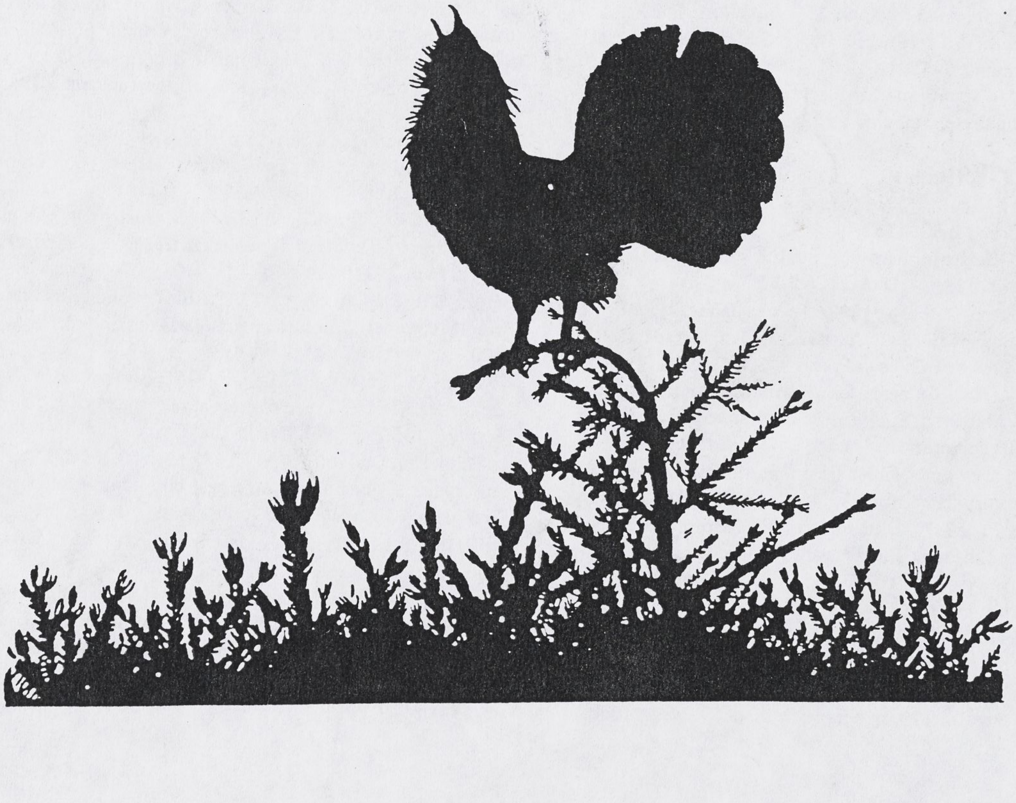

MANAGEMENT AS EXPERIMENTATION

notes for

AN ADDRESS TO GRADUATES IN NATURAL RESOURCES
COLORADO STATE UNIVERSITY, 1994

Carl Walters
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University of British Columbia
Vancouver, B.C. V6T1Z4

Most of you are about to seek jobs with public agencies and other institutions charged with management of renewable resources. You probably think that your education here at CSU has equipped you with a good understanding of at least the basic aims and tools that constitute good management. And indeed it has; I have looked at and participated in many other educational programs around the world, and I have never once regretted having chosen CSU for my own graduate studies.

You are due for a very rude awakening. You will not be on the job long before you start to notice some really shocking things about the people you work with and the problems you supposedly are trying to solve. First, you will make a rather obvious discovery about the Peter Principle: many of the people around you will have risen in the agency to positions that they are not competent to fill. Next you will discover a profoundly important symptom of incompetence: people who box themselves in with rules and procedures to avoid the discomfort of having to make judgements and hard decision choices. Most of the clever ideas and approaches that you suggest will meet with reactions like "we don't have funding for that in this year's budget, but we will take it under advisement" or "that change is too radical and would weaken our credibility with user groups", or "our existing procedures are already perfectly adequate to the task".

Luckily the instiutional problems are not insurmountable. With dedication and perserverence, you will find that the incompetents gradually yield to your suggestions, especially if you are clever about gaining user group and public support for your ideas. In particular, you will make the very pleasant discovery that many resource users are not as greedy, narrow-minded, and short-sighted as they are often portrayed by resource managers who are seeking someone to blame for past mismanagement.

But now you will begin to discover the real and deeper legacies of our incompetence as resource managers. You will see harvest rate policies that bear no obvious relationship to what you have learned about calculating sustainable harvests in population dynamics and harvest scheduling courses, and that appear to have been based on silly models and errors in interpretation of historical data. You will discover that the historical data that are so crucial to establish trends and performance assessments are either entirely lacking or have been gathered in such an inconsistent manner as to prevent you from even assessing broad trends. You will find bitter debate among scientists about the ecological mechanisms responsible for whatever trends are evident, and you will be utterly unable to resolve these debates because the effects of various explanatory factors are all confounded in the data (nature never varies just one factor at a time for you). You will find user groups aligned with whatever scientific explanation best rationalizes whatever they want to do, eg blame the fish stock decline on climatic change rather than overfishing, if you want to keep fishing. And finally you will find the public demanding your scientific advice about how to manage for ecological attributes that nobody used to worry about, like "biodiversity" and spotted owls, and about which your ecology textbooks will have almost nothing useful to say.

In short, you are about to go out into a world where the standard management prescriptions have largely failed, where we really don't know what the best baseline or standard operating procedure and approach should be, and where your profession and agency has very little public credibility. Now, you can join the ranks of professionals who are trying desperately to cover up this situation by pretending to develop "strategic management plans", thick assessment reports, and other bureaucratic reactions. Or, you can follow your conscience by facing up to uncertainty and trying to figure out how to deal honestly with it.

Here are a few suggestions about how to follow that much more difficult road that has come to be called the "adaptive approach to management": (1) begin by explicitly and publicly admitting your ignorance, and seek a broad range of opinions in trying to define clearly just where the important gaps in your understanding are (ie, identify the basic alternative hypotheses that could explain what has been happening, and don't try to decide which of these is most likely or that you personally should "believe" or adopt); (2) reject the notion of a standard or baseline management option, and instead treat every option as a highly uncertain experimental treatment; (3) design your management experiments properly, using the concepts you learned in statistics about control, replication, and measurement; (4) face up to the massive measurement and monitoring requirements that a truly experimental approach will require, and seek real partnerships with resource users and local communities to accomplish the information gathering.

This last recommendation in particular is a radical departure from the way we have traditionally gone about the business of doing natural resource management. By making the arrogant (and incorrect) assumption that only we, as highly trained professionals, are competent to measure what is going on in the field, we have passed up all sorts of opportunities to have large numbers of people help gather the data we need. Indeed, this raises a broader issue about where responsibility and authority for resource management should rest in general. Clearly, public agency involvement is necessary for regional planning and for management of large natural populations, particularly migratory species like waterfowl and salmon. But in North America, we have relied entirely too much on public agencies to do policy development, monitoring, and enforcement that local communities could often do better for themselves.

Fish/Wildlife director leaves a legend of compromise

By The Associated Press

SANTA ANA, Calif. — Gail Kobetich, a Fish and Wildlife Service supervisor who crafted influential and embattled compromises for saving endangered species, has retired from the federal agency.

His efforts helped shape wilderness preserves across Southern California, but they have drawn increasing fire from conservationists dismayed at continuing loss of habitat to housing tracts and strip malls.

No successor has been named for the 60-year-old Kobetich, who retired Friday after four years as head of the U.S. Fish and Wildlife Service's office in Carlsbad.

During that time, he planned and helped create several multispecies reserves in Orange County and San Diego County.

Developers, as well as top Clinton Administration officials, praised his compromise approach, which allows builders to destroy native habitat without bureaucratic hassles as long as they set aside other land for disappearing plants and animals.

Interior Secretary Bruce Babbitt held up the approach as a national model because it aims to preserve whole ecosystems before they become threatened or endangered.

"The whole idea of large-scale conservation planning has been a huge thing," Kobetich said. "It's changed the entire direction of the way the Fish and Wildlife Service approaches conservation."

In his view, cutting deals with landowners and developers amounts to facing economic reality in Southern California: Houses and businesses will be built anyway, and some habitat will be destroyed.

"I guess you would call it a practical approach," Kobetich said. "We can't stop development. We can't buy all the private property out there. Therefore, you negotiate the best deal you can get."

Kobetich has changed direction from his younger days, when he believed species must be saved whatever the cost.

"I used to have a much more rigid viewpoint," he said. "Over the years, I've come to realize that I gained less conservation from a rigid approach."

Kobetich's critics say that was exactly the problem.

"He lost his soul and the green fire died a long time ago," said Leeona Klippstein of Spirit of the Sage Council. "That's when he should have retired."

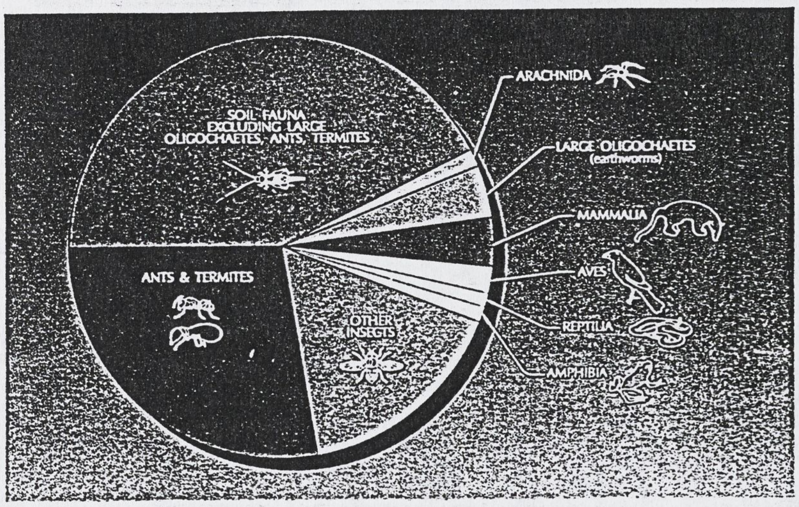
Klippstein's group opposes further construction of roads and houses in Southern California's rapidly vanishing back country. And the disagreement seemed to focus on methods rather than aims.

"The undeveloped part of Orange County is truly glorious from a national-landscapes point of view," Kobetich said. "It would be a true tragedy for the citizens of Orange County, and Southern California in general, if at least a large percentage of what is left is not preserved."

Kobetich and his wife, McSene, are retiring to the Sacramento area, where the family spent 18 years.

ate amounts of hybridization occur among natural populations, or where ordinary sexual reproduction has been replaced entirely or in part by self-fertilization or parthenogenesis.

New species are usually created in one of two ways. A large minority of plant species came into existence in one step, through polyploidy. This is a simple multiplication in the number of gene-bearing chromosomes, sometimes within a preexisting species and sometimes in the hybrids that infrequently



TOTAL ANIMAL BIOMASS

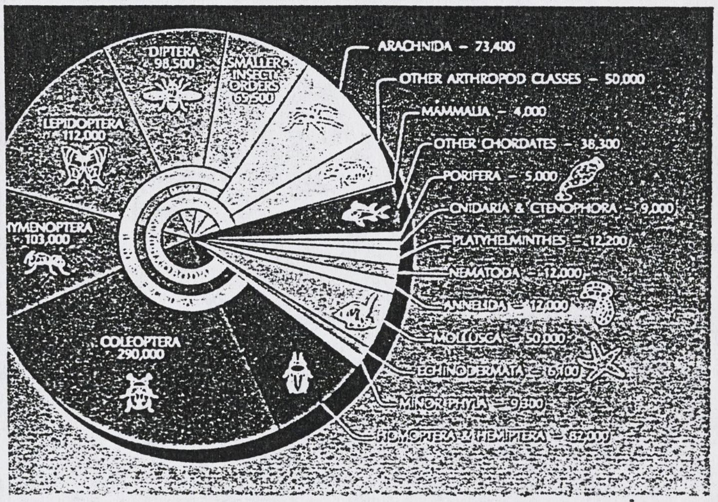
Figure 4. The apportionment of biomass, measured in dry weight, among groups of animals in a rain forest near Manaus, Brazil. [source: Fittkau, E. J. & Klinge, H. 1973. On biomass and trophic structure of the central Amazonian rain forest ecosystem. *Biotropica* 5:2–14]

occur between two species. Polyploids formed this way are typically unable to breed back to the parent species to produce fertile offspring.

The second major generative process, geographic speciation, takes much longer. It starts when a single population (or series of populations) is divided by some barrier extrinsic to the organisms, such as a river, mountain range, or arm of the sea. The isolated populations then diverge from each other in evolution because of adaptation to the inevitable environmental differences on either side of the barrier. Since all populations evolve if given enough time, divergence between all extrinsically isolated populations must eventually occur. By this process alone the populations can acquire enough differences to reduce interbreeding between them should the extrinsic barrier be removed and the population again come into contact. If sufficient differences have accu-

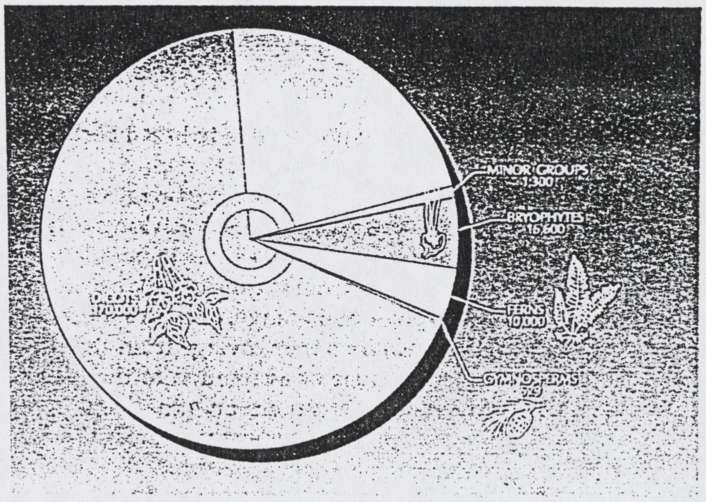
ıen confined in captivity, but during historical at least, they have never interbred where they ogether in the wilds of southern Asia. Hence, hough lions and tigers are capable of hybrid-, they comprise two different species.

'he biological species concept is the best ever d, but it remains less than ideal. It works very r most animals and some kinds of plants, but e replaced with arbitrary divisions in many lants (and in a few animals) where intermedi-



ıIMALS: TOTAL SPECIES, 1,032,000

ıure 2. The number of living animal species known at the present cording to major taxonomic group.



ıHER PLANTS: TOTAL SPECIES, 248,000

re 3. The number of living species of higher plants known at ıt time, according to major taxonomic group.

Sinking Ark

Denver Post
editorial

- Reauthorize ESA
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Evol. in Special Creation
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Cancer

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1177. Harper's 258(1542)

R. T. Mutti

THE SINKING ARK

Protecting God's creatures two by two

by William Tucker

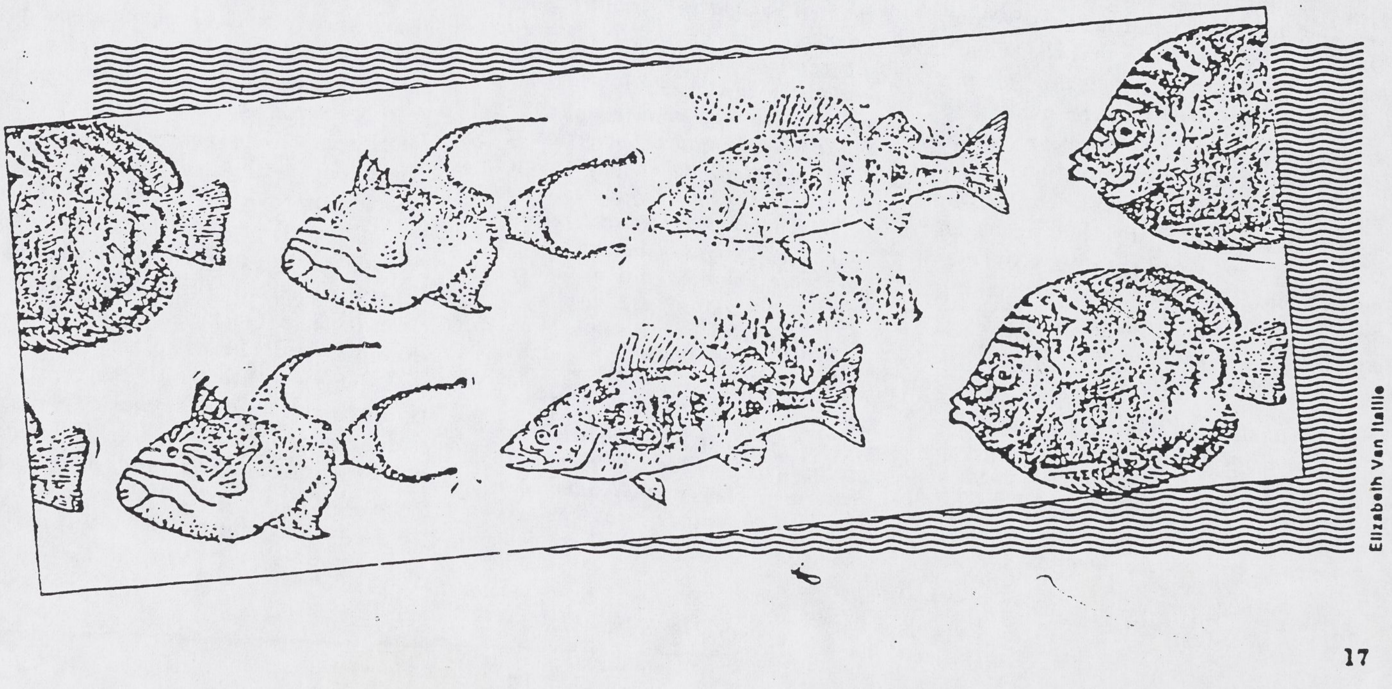
THE LATEST ENVIRONMENTAL crisis turns upon the protection of endangered species from the onslaught of human economic aspirations. Once again, institutions like the Sierra Club and the World-Watch Institute have rushed to the fore, telling us we must all change our "life styles," think small, live beautifully, and try to hang on desperately to what we have without rocking the ecological lifeboat. "Noah's Ark is sinking," the environmentalists tell us. We are chopping away at the evolutionary tree where we sit precariously perched among the top branches. Our human activity is about to destroy the genetic diversity of the creation, leaving us stranded at the tip of a slender, catastrophe-prone stalk of ecological singularity. The only salvation is to call a halt to any further development in order to conduct studies of its potentially devastating effects. Naturally, this solution is more attractive to those people who are satisfied with what they already have than to those who hope to move up a few more rungs on the economic ladder.

William Tucker is a contributing editor of Harper's.

Does the scenario of "eco-catastrophe" bear any resemblance to biological reality? I think not, and I think when the terms of the argument are clearly understood, it will seem almost absurd that Congress, the bureaucracy, and the Supreme Court have been duped into trying to pass and enforce a law like the 1973 Endangered Species Act that makes it almost impossible for a farmer to drive his tractor across a field without threatening some "eco-catastrophe."

1 What does the term "species" actually mean? The system of biological classification, set up originally by the eighteenth-century Swedish naturalist Linnaeus, divides all living things into seven major categories. They are: kingdom, phylum, class, order, family, genus, and species. Human beings, for example, belong to the kingdom of animals, phylum of chordates, class of mammals, order of primates, family of hominids, genus homo, and species *Homo sapiens*. The passion of naturalists and taxonomists for finer and finer distinctions has further embellished the system, however, so that each major category now includes "sub-," "super-," and "infra-" groups as well. Thus, the classifications *below* the species level now read as follows: species, subspecies (race), variety, and population. The Endangered Species Act of 1973, despite its title, actually protects groups of plants and animals right down to the level of "populations"—a A biological term that simply refers to a group of animals or plants that happen to live in a particular location, and could refer to just two animals.

When a person thinks of "species," such animals as deer, bears, elephants, skunks, and sharks are likely to come to mind. In fact, these animals are grouped either at the genus or family levels. Elephants are a family of animals with two genera and two species. Bears are a family with about eight species. There are forty species of deer, twelve of which in North America are called "elk." An oriole is a genus with fifteen species and a crow a genus with thirty-six species. There are about ten species of skunks, a dozen species of



Elizabeth Van Halle

weasels, 150 species of squirrels, 850 species of bats, and 350 species of sharks. The giraffe is an animal that comes closest to the commonsense notion of "species." It is a single genus with a single species.

The numbers stay fairly manageable when we stick to mammals and birds, which most taxonomists agree have been rather thoroughly described and classified. But with fish, the number of species begins to multiply beyond commonsense proportions, and when the invertebrates are counted—particularly insects—the numbers become understandable only in powers of ten. It is estimated, for example, that there are about 10,000 described species of fresh-water fish, with perhaps another 5,000 that have not yet been identified. Within the invertebrate phylum, no estimates of the number of species not yet described have been attempted, but at present biologists have identified about 5,300 corals, 4,800 sponges, 2,000 oysters, 50,000 mites and spiders, and 10,000 nematodes, microscopic worms that sometimes infest crops. Among insects, about 360 species of dragonflies have been observed, 1,100 species of butterflies in North America alone, and about 16,000 species of flies. It is not uncommon for a single insect specialist to have identified more than 1,000 new species in his career, and the number of new species described each year by all naturalists is about 10,000.

By 1815 THE VARIOUS species of plants and animals listed by diligent naturalists had become so numerous that Samuel Taylor Coleridge wrote that the science of natural history was about to collapse under its own weight. The man who brought some order and rationality to this gargantuan encyclopedia of minute classifications was Charles Darwin, and it is not surprising that he began *The Origin of Species* with a frontal assault on the importance of making fine distinctions between the various species. In his second chapter Darwin wrote:

> *How many of the birds and insects in North America and Europe, which differ very slightly from each other, have been ranked by one eminent naturalist as undoubted species, and by another as varieties, or, as they are often called, geographical races!... Close investigation, in many cases, will no doubt bring naturalists to agree how to rank doubtful forms. Yet it must be confessed that it is in the best known countries that we find the greatest number of them.* I have been struck with the fact that if any animal or plant in a state of nature be highly useful to man, or from any cause closely attracts his attention, varieties of it will almost universally be found recorded. These varieties, moreover, will often be ranked by some authors as species. [*emphasis added*]

Darwin argued that these apparently discrete varieties among plants and animals are in fact closely related through common ancestry. Diversification among the species reflects the small adaptive changes that animals evolve as they compete in their particular environments. "I look at the term species as one arbitrarily given," he wrote, "for the sake of convenience ... to a set of individuals closely resembling each other ... species are only strongly marked and permanent varieties."

After the rediscovery in 1901 of Mendel's work on genetics, the mechanics of evolutionary diversity became clear, and in the 1920s and '30s a group of English scientists, led by Julian Huxley, restated Darwin in terms of genetic theory. "The chief method of origin [of new species] is through physical isolation," Huxley wrote.

> *Once two groups are physically isolated so that they can no longer interbreed, they inevitably come to diverge from each other in the new mutations and gene-recombinations which they accumulate under the influence of natural selection....*
>
> *In addition, when an isolated group is small in numbers, it can be shown on mathematical grounds that it is likely to pick up and incorporate some mutations and recombinations that are useless or even slightly unfavorable. Thus, some of the diversity of life is, biologically speaking, purely accidental....*
>
> *The result is an overwhelming multiplicity of distinct species. Naturally, they are all adapted to their surroundings, but the geographical and cytological accidents that produced physical and genetic isolation cause their numbers to be much greater than that which would be necessary on purely adaptive grounds; and non-adaptive variation adds its quota to the diversity.*
>
> *Most of evolution is thus what we may call short-term diversification....*

Thus, evolutionary theory, properly understood, maintains that *anywhere* that small populations have become isolated, some physical and genetic differences—not all of them significant to the population survival—will have evolved. The theory is sometimes stated that these separate "species" are incapable of interbreeding, but in practice this criterion has long since been abandoned. Hundreds of distinct species can interbreed to produce offspring: lions and tigers; wolves and coyotes; sunfish and bass; and nearly all the world's eight species of wild and domestic cattle—including buffalo. The criterion has thus been modified to say that two animal populations can be considered separate species if they do not interbreed *in the wild*. Under this system, it would be easy to classify the human populations of New Guinea and Sweden as distinct species.

sympatric

THE ARMIES OF NATURALISTS in search of the honor of naming a new species were hardly checked by Darwin's restraining criticism, and the number of new species has continued to multiply over the years. Birds and mammals, because they do not breed very fast, have produced relatively few varieties. But fish and invertebrates, which produce millions of eggs each year, raise the chances of finding small isolated populations, varieties, and even "endangered species" to nearly 100 percent. The odds are thus in favor of people who disapprove of dams and other public works projects for reasons of politics or self-interest, and who can enlist the scientific skills of like-minded naturalists to block such projects. For example, "endangered species" of snails and clams are threatening the construction of dams in the Tennessee Valley; endangered insects are blocking water projects in Colorado, and an endangered species of butterfly is obstructing an airport expansion in Los Angeles.

In fact, engineers could probably save themselves the trouble of beginning such projects right now by acknowledging that anywhere naturalists look they are likely to discover some unique plant or animal that will be entitled to the protection of federal law.

Just how easily these small populations of plants and animals can be put to political use can be illustrated by the case of the snail darter, which A the U.S. Supreme Court recently ruled must be protected at the cost of scrapping the nearly completed $3 million Tellico Dam across the Little Tennessee River. The snail darter was discovered by David Etnier, an outstanding icthyologist (fish specialist) at the University of Tennessee, who makes no secret that he does not like the Tennessee Valley Authority's proposed dam. "Most of these big dams are turkeys," Dr. Etnier told me in a telephone interview last October. "They're a big waste of the taxpayers' money. They're big pork-barrel projects that don't do anybody any good. I just generally have an aversion to projects that would alter our few remaining big free-flowing rivers."

Dr. Etnier had been a key witness for the Environmental Defense Fund, a Washington-based environmental group that worked with Tennessee landowners who were fighting condemnation of their property and succeeded in delaying the project over a year from 1972–73. Soon after the Endangered Species Act of 1973 said that all new projects *must* give way to endangered animal and plant populations, Dr. Etnier set out to find just such a small population in the Little Tennessee River.

"We went down to the lower twenty miles of the river with masks and snorkels, and on my very first dive I saw something unusual curled up on the bottom," Dr. Etnier told me. "I expected it to move away, but it stayed right there. When I brought it to the surface and had a look, I knew I had something that no human being had ever seen before."

3 The fish turned out to be a member of the subgenus *Imostoma*, which includes five species of darters, two of which have been described by Dr. Etnier. The entire genus belongs to the perch family, of which there are eight genera, and more than 150 species. Within the three genera that include the "darters," there are more than 100 species, sixty-five of which live in the Tennessee River Valley Basin. There is little to distinguish them, and only trained icthyologists who specialize in darters can tell them apart.

In January, 1975, Dr. Etnier published a paper describing the new species in the *Proceedings of the Biological Society of Washington*, a journal published quarterly by a group of scientists within the Smithsonian Institution (although not a Smithsonian publication). The paper described the snail darter as a species living in isolation in the lower portion of the Little Tennessee River, that is unique because it eats a snail that inhabits that portion of the river and because it has several fin and scale characteristics that, although found in other species of darters, are not found in the same combination. Dr. Oliver Flint, a forty-seven-year-old insect specialist and vice-president of the Society, explained the procedure in a telephone interview last October.

"Our publication has a circulation of about 550 copies, 225 of which go to libraries," he told me. "We publish twenty to twenty-five articles each issue, and 99 percent of these are describing new species. All the papers are refereed by other scientists, but we rarely have a rejection. We usually ask an author to make some revisions if there is any problem. There are probably over 100 journals in the country that are similar to ours.

"I'm sure there is plenty of room for opinion in some of these new species, but we rarely, if ever, have a paper that's challenged. The question is whether the discovery is something new and different, or just something that was never found in that particular place before. I sometimes have my doubts about a lot of these new species. Granted there's little difference B here and there, but perhaps it's just another population on this particular mountain or on that particular river. There are rules published by the International Commission of Zoological Nomenclature in London, but I think the book is out of print right now. When you get down to this level of population, though, it's almost impossible to prove anything, since wild animals almost never breed under captivity. When you start talking about insects, it almost doesn't matter if you call it a new species, since there are already so many anyway."

Despite this rather haphazard state of affairs in the international listing of new species, Dr. Etnier's description of the snail darter has been acknowledged by TVA biologists as legitimate. The scientists challenged the listing for awhile, but now admit that the snail darter is indeed a unique population with characteristics shared by no other fish.

Is THERE ANY WAY THAT the concern over endangered species can be redefined in some more rational manner, so that the legitimate worries about our impact on the natural environment can be reconciled with a reasonable amount of social and economic progress, without giving way to the spectacle of hordes of environmental activists finding "endangered species" of worms, snails, and insects under every rock and tree? I think there is.

First, the compass of the current law should not extend beyond the species level for reptiles, mammals, and birds. (The 1977 amendment to the law limited its reach to "sub-species" for invertebrates, but left it at "population" for vertebrates). Because these species do not breed rapidly, they have developed relatively few varieties, and the genetic resources they represent should not be lost.

butterflies

gophers

mice

Second, for all other orders of plants and animals, the "survival" cutoff could be placed at the genus level. Many plants and animals are genera with a single species—i.e., they have few close relatives, and should be protected. But invertebrates, in particular, are so abundant and prolific that they hardly seem to need protection at the species level. This does not mean that invertebrates are not important to human beings, or to the "ecosystem." Environmentalists are fond of citing the horseshoe crab (a "living fossil" that has not changed significantly for thousands of years) as an animal that has recently been found to have unexpected medical significance: its blood can be used to detect toxins in intravenous fluids. However, the horseshoe crab is neither a species, nor is it endangered. Horseshoe crabs are a family of animals with about twenty species that are abundant all along the Atlantic Coast and in the South Pacific. The bread molds that produce penicillin are also frequently cited as "small but important" creatures, yet here the environmentalists strain the imagination. Bread molds are ubiquitous in nature, and we probably couldn't wipe them out if all our human resources were devoted to the effort.

phyl / genus

unit

intraspec

adaptive unit

There is no need to argue social Darwinism, or to talk about "survival of the fittest" and "nature red in tooth and claw" in order to cut a path through the maze of law and confusion that now surrounds the concern about endangered species. Efforts can be made to alter projects or reestablish unique species, and in fact this approach has worked in almost all of the cases that have resulted from the 1973 law. The statute still reads, however, that in cases where there is no possible resolution, the project must give way. Even though Congress has now established a federal review board to resolve such impasses, it seems unlikely that the committee will be able to accomplish much until Congress recognizes what a "species" or a "population" of plants or animals really is. Where it is decided that a project cannot possibly be built without obliterating some local population or species, there are at least two powerful arguments that make it extremely unlikely that we are creating an evolutionary catastrophe.

First, where creatures are unique only as "species," they are bound to have many close relatives with whom they share most of their important genetic characteristics. But second, if a species has evolved some trait observed in no other creature, it is extremely unlikely that it could have strong evolutionary significance—otherwise it would have created an evolutionary advantage that would have caused the species to proliferate widely. The Environmental Defense Fund, for example, has argued that the snail darter produces an enzyme capable of detaching the snail from its shell so the animals can be eaten without crushing the shell, as other species of darter must do. Yet other fish eat the same snails using different enzymes and different methods, and this particular trait does not seem to promise any wide evolutionary advantage. Had some small group of animals or plants developed a method of curing cancer cells in their bodies, on the other hand, it is almost impossible that the trait would have remained with that small group since the survival advantage would have caused their genes to proliferate widely.

But still, the environmentalists tell us, we are setting ourselves up for "eco-catastrophe" because any degradation of the genetic base makes the ecosystem more fragile. Diversity equals stability, is the way this argument is usually phrased. It is one of the real embarrassments of the environmental effort that this "ecological commandment" widely stated in the popular literature is completely unproven, and in many cases is demonstrably false. If a mature forest is temporarily cleared, for example, a wide variety of organisms will rapidly compete for succession, but will gradually give way again to a less diversified but far more stable collection of "climax" species. Diversity does not always equal stability and the formula only seems to hold true in the most extreme cases.

Ultimately, the case for protecting every plant and animal population and species is argued in terms of religious guilt. Do we want to be the first people in history to consciously and deliberately eliminate a species? I hope it is clear that this question does not appeal to a rational assessment of the evolutionary consequences, but to emotion and doubt. What the question in fact asks is: Should we kill any living creature? One answer is, of course, that we sometimes have to. The evolutionary cathedral could not have come into existence if some creatures had not been destroyed by others, and if all the species that ever evolved had survived until now, there wouldn't be room on the planet to support them all.

Extinction has been the common fate of nearly all the species that have evolved on earth. We ourselves are a part of nature, and it is impossible for us to live without changing it to some degree. If we are to adopt the attitude of Indian holy men and live in fear of putting our feet down because we might crush some living creature, we should at least be aware that such *unadaptability* frequently occurs in nature. It is nearly always a highly unsuccessful evolutionary strategy. □

Uncertainty, Resource Exploitation, and Conservation: Lessons from History

Donald Ludwig, Ray Hilborn, Carl Walters

There are currently many plans for sustainable use or sustainable development that are founded upon scientific information and consensus. Such ideas reflect ignorance of the history of resource exploitation and misunderstanding of the possibility of achieving scientific consensus concerning resources and the environment. Although there is considerable variation in detail, there is remarkable consistency in the history of resource exploitation: resources are inevitably overexploited, often to the point of collapse or extinction. We suggest that such consistency is due to the following common features: (i) Wealth or the prospect of wealth generates political and social power that is used to promote unlimited exploitation of resources. (ii) Scientific understanding and consensus is hampered by the lack of controls and replicates, so that each new problem involves learning about a new system. (iii) The complexity of the underlying biological and physical systems precludes a reductionist approach to management. Optimum levels of exploitation must be determined by trial and error. (iv) Large levels of natural variability mask the effects of overexploitation. Initial overexploitation is not detectable until it is severe and often irreversible.

In such circumstances, assigning causes to past events is problematical, future events cannot be predicted, and even well-meaning attempts to exploit responsibly may lead to disastrous consequences. Legislation concerning the environment often requires environmental or economic impact assessment before action is taken. Such impact assessment is supposed to be based upon scientific consensus. For the reasons given above, such consensus is seldom achieved, even after collapse of the resource.

For some years the concept of maximum sustained yield (MSY) guided efforts at fisheries management. There is now widespread agreement that this concept was unfortunate. Larkin (*1*) concluded that fisheries scientists have been unable to control the technique, distribution, and amount of fishing effort. The consequence has been the elimination of some substocks, such as herring, cod, ocean perch, salmon, and lake trout. He concluded that an MSY based upon the analysis of the historic statistics of a fishery is not attainable on a sustained basis. Support for Larkin's view is provided by a number of reviews of the history of fisheries (*2*). Few fisheries exhibit steady abundance (*3*).

It is more appropriate to think of resources as managing humans than the converse: the larger and the more immediate are prospects for gain, the greater the political power that is used to facilitate unlimited exploitation. The classic illustrations are gold rushes. Where large and immediate gains are in prospect, politicians and governments tend to ally themselves with special interest groups in order to facilitate the exploitation. Forests throughout the world have been destroyed by wasteful and shortsighted forestry practices. In many cases, governments eventually subsidize the export of forest products in order to delay the unemployment that results when local timber supplies run out or become uneconomic to harvest and process (*4*). These practices lead to rapid mining of old-growth forests; they imply that timber supplies must inevitably decrease in the future.

Harvesting of irregular or fluctuating resources is subject to a ratchet effect (*3*): during relatively stable periods, harvesting rates tend to stabilize at positions predicted by steady-state bioeconomic theory. Such levels are often excessive. Then a sequence of good years encourages additional investment in vessels or processing capacity. When conditions return to normal or below normal, the industry appeals to the government for help; often substantial investments and many jobs are at stake. The governmental response typically is direct or indirect subsidies. These may be thought of initially as temporary, but their effect is to encourage overharvesting. The ratchet effect is caused by the lack of inhibition on investments during good periods, but strong pressure not to disinvest during poor periods. The long-term outcome is a heavily subsidized industry that overharvests the resource. Grazing fee 1.35 - corporate ranch

The history of harvests of Pacific salmon provides an interesting contrast to the usual bleak picture. Pacific salmon harvests rose rapidly in the first part of this century as markets were developed and technology improved, but most stocks were eventually overexploited, and many were lost as a result of overharvesting, dams, and habitat loss. However, in the past 30 years more fish have been allowed to spawn and high seas interception has been reduced, allowing for better stock management. Oceanographic conditions appear to have been favorable: Alaska has produced record catches of salmon and British Columbia has had record returns of its most valuable species (*5*).

mining

We propose that we shall never attain scientific consensus concerning the systems that are being exploited. There have been a number of spectacular failures to exploit resources sustainably, but to date there is no agreement about the causes of these failures. Radovitch (*6*) reviewed the case of the California sardine and pointed out that early in the history of exploitation scientists from the (then) California Division of Fish and Game issued warnings that the commercial exploitation of the fishery could not increase without limits and recommended that an annual sardine quota be established to keep the population from being overfished. This recommendation was opposed by the fishing industry, which was able to identify scientists who would state that it was virtually impossible to overfish a pelagic species. The debate persists today. experts

After the collapse of the Pacific sardine, the Peruvian anchoveta was targeted as a source of fish meal for cattle feed. The result was the most spectacular collapse in the history of fisheries exploitation: the yield decreased from a high of 10 million metric tons to near zero in a few years. The stock, the collapse, and the associated oceanographic events have been the subject of extensive study, both before and after the event. There remains no general agreement about the relative importance of El Niño events and continued exploitation as causes of collapse in this fishery (*7*).

sci.-sound mgt.

The great difficulty in achieving consensus concerning past events and a fortiori in prediction of future events is that controlled and replicated experiments are impossible to perform in large-scale systems. Therefore there is ample scope for differing interpretations. There are great obstacles to any sort of experimental approach to management because experiments involve reduction in yield (at least for the short term) without any guarantee of increased yields in the future (*8*). Even in the case of Pacific salmon stocks that have been extensively monitored for many years, one cannot assert with any confidence that present levels of exploitation are anywhere near optimal because the requisite experiments would

(*Continued on page 36*)

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(Continued from page 17)

involve short-term losses for the industry (9). The impossibility of estimating the sustained yield without reducing fishing effort can be demonstrated from statistical arguments (10). These results suggest that sustainable exploitation cannot be achieved without first overexploiting the resource.

The difficulties that have been experienced in understanding and prediction in fisheries are compounded for the even larger scales involved in understanding and predicting phenomena of major concern, such as global warming and other possible atmospheric changes. Some of the time scales involved are so long that observational studies are unlikely to provide timely indications of required actions or the consequences of failing to take remedial measures.

Scientific certainty and consensus in itself would not prevent overexploitation and destruction of resources. Many practices continue even in cases where there is abundant scientific evidence that they are ultimately destructive. An outstanding example is the use of irrigation in arid lands. Approximately 3000 years ago in Sumer, the once highly productive wheat crop had to be replaced by barley because barley was more salt-resistant. The salty soil was the result of irrigation (11). E. W. Hilgard pointed out in 1899 that the consequences of planned irrigation in California would be similar (12). His warnings were not heeded (13). Thus 3000 years of experience and a good scientific understanding of the phenomena, their causes, and the appropriate prophylactic measures are not sufficient to prevent the misuse and consequent destruction of resources.

Some Principles of Effective Management

Our lack of understanding and inability to predict mandate a much more cautious approach to resource exploitation than is the norm. Here are some suggestions for management.

1) Include human motivation and responses as part of the system to be studied and managed. The shortsightedness and greed of humans underlie difficulties in management of resources, although the difficulties may manifest themselves as biological problems of the stock under exploitation (2).

self interest

2) Act before scientific consensus is achieved. We do not require any additional scientific studies before taking action to curb human activities that effect global warming, ozone depletion, pollution, and depletion of fossil fuels. Calls for additional research may be mere delaying tactics (14).

3) Rely on scientists to recognize problems, but not to remedy them. The judgment of scientists is often heavily influenced by their training in their respective disciplines, but the most important issues involving resources and the environment involve interactions whose understanding must involve many disciplines. Scientists and their judgments are subject to political pressure (15).

multiple use

4) Distrust claims of sustainability. Because past resource exploitation has seldom been sustainable, any new plan that involves claims of sustainability should be suspect. One should inquire how the difficulties that have been encountered in past resource exploitation are to be overcome. The work of the Brundland Commission (16) suffers from continual references to sustainability that is to be achieved in an unspecified way. Recently some of the world's leading ecologists have claimed that the key to a sustainable biosphere is research on a long list of standard research topics in ecology (17). Such a claim that basic research will (in an unspecified way) lead to sustainable use of resources in the face of a growing human population may lead to a false complacency: instead of addressing the problems of population growth and excessive use of resources, we may avoid such difficult issues by spending money on basic ecological research.

tech fix

deterministic models

5) Confront uncertainty. Once we free ourselves from the illusion that science or technology (if lavishly funded) can provide a solution to resource or conservation problems, appropriate action becomes possible. Effective policies are possible under conditions of uncertainty, but they must take uncertainty into account. There is a well-developed theory of decision-making under uncertainty (18). In the present context, theoretical niceties are not required. Most principles of decision-making under uncertainty are simply common sense. We must consider a variety of plausible hypotheses about the world; consider a variety of possible strategies; favor actions that are robust to uncertainties; hedge; favor actions that are informative; probe and experiment; monitor results; update assessments and modify policy accordingly; and favor actions that are reversible.

revised "scientific method"

Political leaders at levels ranging from world summits to local communities base their policies upon a misguided view of the dynamics of resource exploitation. Scientists have been active in pointing out environmental degradation and consequent hazards to human life, and possibly to life as we know it on Earth. But by and large the scientific community has helped to perpetuate the illusion of sustainable development through scientific and technological progress. Resource problems are not really environmental problems: They are human problems that we have created at many times and in many places, under a variety of political, social, and economic systems (19).

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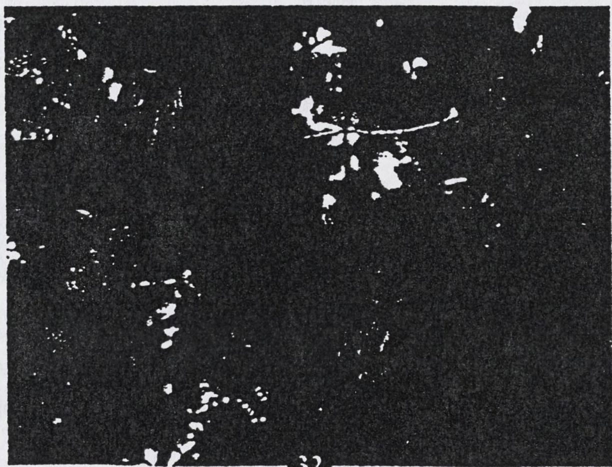
DEFENDERS

ON THE COVER

A group of gray wolves in a captive population in Bavarian Forest National Park, Germany. The photo is by Gunter Ziesler/Peter Arnold, Inc. Germany has only a few wild wolves, but a number of European countries have significant although in most cases hard-pressed populations, a DEFENDERS global wolf survey shows. On page 6, Don Hinrichsen reports on the numbers and status of this most fabled of the world's large carnivores.

FEATURES



FLEDGLING CACTUS FERRUGINOUS PYGMY OWLS. MICHAEL J. TERRIO

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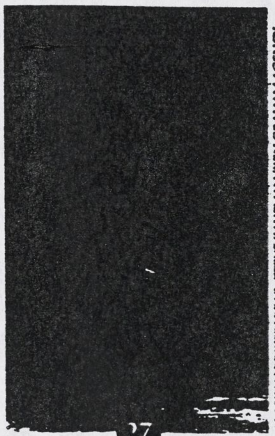


ALASKAN BROWN BEAR. STEVE KAUFMAN/KEN GRAHAM AGENCY

27

DEPARTMENTS

Farm Bureau vs. Nature

The attack on Yellowstone's wolves is part of a sweeping anti-environmental campaign

BY VICKI MONKS

OUT IN THE Apache National Forest on the Arizona-New Mexico border, Mexican wolves reintroduced last March are already running into trouble. "The wolves are threatening people," Eric Ness of the New Mexico Farm and Livestock Bureau (NMFLB) charges. It seems that some visitors to a guest ranch in the area heard the wolves howling somewhere off in the forest. That scared these people? "If a wolf is howling outside your door, that's threatening enough for me," Ness says.

Ness's characterization of this incident as a threat is typical of the hyperbole favored by many of the Farm Bureau activists who have made fights against wolf reintroduction their *cause célèbre.* NMFLB is an affiliate of the American Farm Bureau Federation, which filed a 1994 lawsuit seeking to block reintroduction of gray wolves in Yellowstone National Park. That case resulted in a recent court order requiring removal of reintroduced Yellowstone wolves. The government, Defenders of Wildlife and others are appealing the order. Meanwhile, NMFLB has sued to force removal of the Apache wolves.

A search of the Farm Bureau's web site brings up some wild rhetoric. In an essay, Montana Farm Bureau Executive Vice President Jake Cummins argues that environmental leaders "don't care whether the wolves live or die." Environmentalists just want "to expand federal land use control . . . [in order to] redistribute wealth by consolidating power in the federal bureaucracy," Cummins writes. He suggests that such people still admire "the Communist ideal."

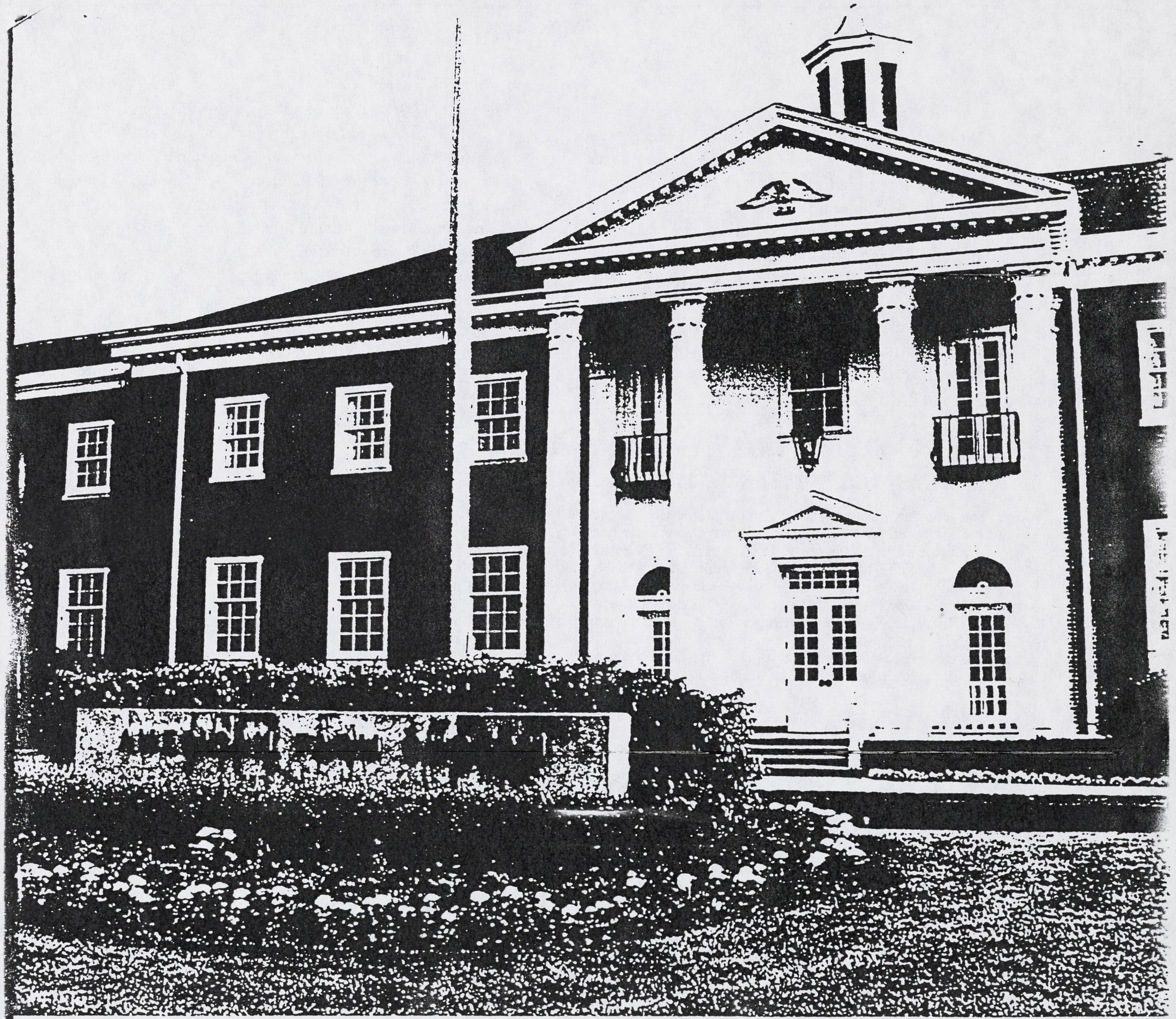
Cummins's grandiloquence may sound over the top, but make no mistake, the Farm Bureau is far from the political fringes. Although most people may be only vaguely aware of the organization, an examination of the American Farm Bureau Federation (AFBF) and its affiliates reveals that this nonprofit organization is a powerful, persistent and wealthy opponent of environmental protection and wildlife conservation – an advocate of right-wing causes that sometimes have little to do with agriculture and at other times may work to the detriment of the family farmers that AFBF claims to represent.

In a *Fortune* magazine survey published last December, the American Farm Bureau Federation ranked 17th among the 25 most powerful special-interest groups in Washington, just below the Veterans of Foreign Wars of the United States and just above the Motion Picture Association of America. It also bested the American Legion, the National Governors' Association and the International Brotherhood of Teamsters. The Farm Bureau stood out as one of the best at manipulating the laws by which we live, the survey said.

With more than 4.7 million members and with affiliated organizations in all 50 states, AFBF wields enormous political power, from Congress to state legislatures and county commissions. "They are an incredibly powerful lobby," says Sam Hitt of Forest Guardians, a Santa Fe, New Mexico, environmental group. Hitt has run up against the Farm Bureau time and again on such issues as wolf reintroduction and protection of streamside ecosystems. "Legislators seem to go google-eyed when they see them walk through the door, and that's caused the loss of a lot of our wildlife heritage," Hitt says.

Defenders of Wildlife biologist Bob Ferris says, "County supervisors in almost all rural areas have some connection to the Farm Bureau. That's where a lot of the decisions about land use and the sorts of things that affect wildlife are made."

The Chamber of Commerce in Binghamton, New York, set up the first county farm bureau in 1911 to act as a sponsor for an extension agent provided by the U.S. Department of Agriculture (USDA). From that time through the 1950s, a cozy relationship developed between the private farm bureaus and USDA agents – a relationship so close that many farmers mistakenly believed the farm bureaus and the government were one and the same, according to a history of the Farm Bureau written by A.V. Krebs. In 1954 USDA ordered an end to its agents' practice of accepting free office space and gratuities from farm bureaus, but close connections between the two



This imposing office building in Park Ridge, Illinois, outside Chicago, is the American Farm Bureau Federation's headquarters.

remained. Ironically, it was this association with the federal government — and the consequent access to federal crop programs and technical information — that helped establish AFBF's dominance as a farmers' organization.

These days, AFBF rails against the intrusiveness of the federal government and especially against environmental regulations, which AFBF claims are overly burdensome to farmers. The Endangered Species Act, wetlands laws, the Clean Air Act, the Safe Drinking Water Act and many other laws have pushed American agriculture to the breaking point, according to AFBF. AFBF's President Dean Kleckner aims particular criticism at the Food Quality Protection Act, which directs the Environmental Protection Agency (EPA) to set standards for pesticide residues in food at levels low enough to protect the health of infants and children. "Sane people do wonder what these kids will eat . . . when the government closes the produce department at our grocery stores," Kleckner wrote in a newspaper column in which he suggested that EPA's "bureaucratic madness" would result in bans on all agricultural chemicals.

Although AFBF calls itself the voice of the American farmer, many of the causes it champions, including less pesticide regulation, relate as much to the Farm Bureau's financial interests as to the needs of farmers. The Farm Bureau may genuinely fear that agriculture will suffer if farmers must reduce their use of chemicals, but Farm Bureau-affiliated companies own stock in corporations that manufacture pesticides, and presumably those investments might suffer as well.

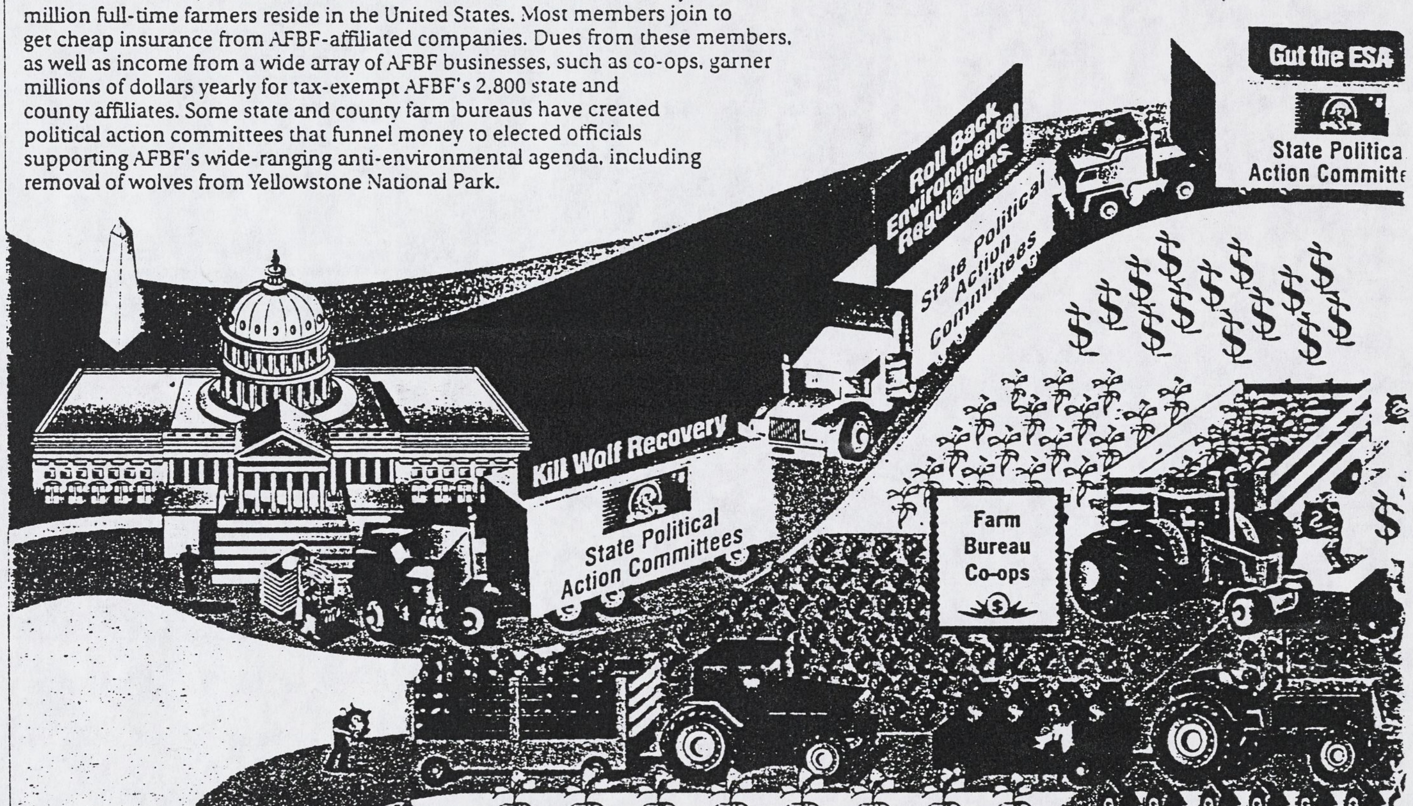
According to corporate documents, 63 Farm Bureau-affiliated insurance companies earn a total of more than $6.5 billion annually in net premiums. The Farm Bureaus also have investments in banks, mutual-fund companies, financial-services firms, grain-trading companies and other businesses. Many of those businesses in turn own stocks in oil and gas, pulp and paper, timber, railroad, automobile, plastics, steel, chemical, pesticide, communications, electronics and cigarette companies and even a nuclear power plant. The lists of stocks owned by Farm Bureau affiliates read like a who's who of corporate heavyweights: Philip Morris, Weyerhaeuser, Union Carbide, DuPont, AT&T, Ford Motor, Raytheon (the world's leading manufacturer of tactical missiles), CBS and many more.

In a recent interview, AFBF Washington lobbyist Dennis Stolte claimed ignorance of these financial interests and insisted that the insurance and other businesses have little to do with AFBF. "That's not the Farm Bureau," he said. "Our members are farmers for the most part. They're people who are interested in promoting agriculture." Nevertheless, comparisons of the boards of directors of Farm Bureau-affiliated businesses and Farm Bureau organizations themselves show substantial overlap. In many cases, the individuals and boards controlling the businesses also control the state farm bureaus. Frequently, much of the profit earned by these businesses reverts to the farm bureaus. In one case in point, the Ohio Farm Bureau reported a profit of $11 million last year.

So vast is this web of interlocking companies with interlock-

AN INFLUENTIAL EMPIRE:
The American Farm Bureau Federation

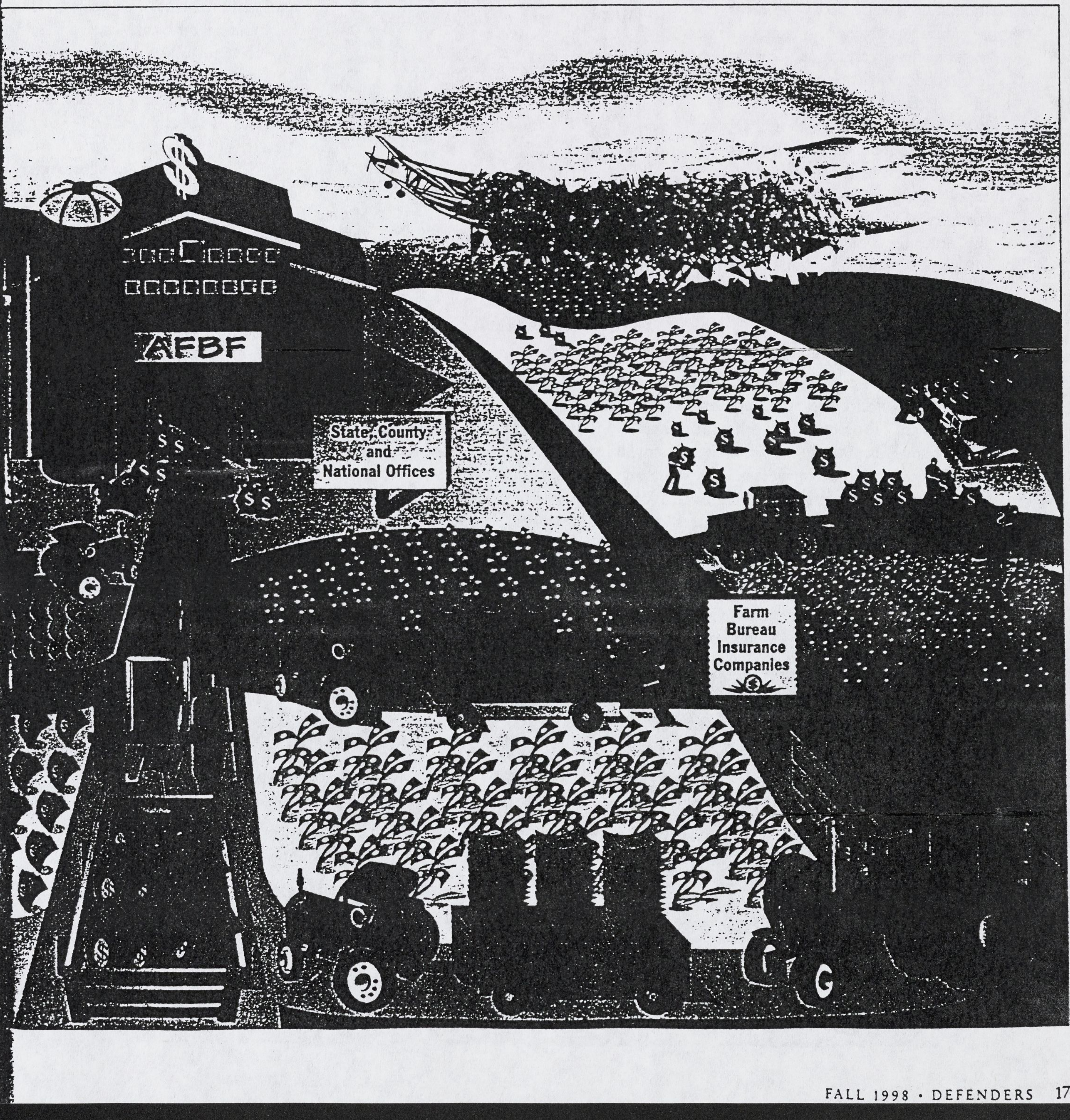
The American Farm Bureau Federation (AFBF) boasts 4.7 million members in all 50 states. However, the bulk of these members are not farmers, as only about 1 million full-time farmers reside in the United States. Most members join to get cheap insurance from AFBF-affiliated companies. Dues from these members, as well as income from a wide array of AFBF businesses, such as co-ops, garner millions of dollars yearly for tax-exempt AFBF's 2,800 state and county affiliates. Some state and county farm bureaus have created political action committees that funnel money to elected officials supporting AFBF's wide-ranging anti-environmental agenda, including removal of wolves from Yellowstone National Park.



ing boards that it is nearly impossible to estimate the true extent of the Farm Bureau's financial power. "There's an impression that this is a huge organization of farmers," says former Texas Agriculture Commissioner Jim Hightower, who now hosts a radio call-in show. "But they are no more a family farmer organization than is State Farm Insurance. Just because you have the word farmer in your name doesn't mean you really represent farmers."

o vast is this web of interlocking companies that it is nearly impossible to estimate the true extent of the Farm Bureau's financial power.

USDA puts the number of full-time American farmers at just over 1 million, so clearly most of AFBF's 4.7 million members must come from outside of agriculture. Numbers from the Texas Farm Bureau (TXFB) tell the story. In 1997, Harris County, which includes metropolitan Houston, had 4,675 members even though USDA listed only 551 full-time farmers there. Dallas County, with just 229 farmers, registered 2,332 Farm Bureau members.



DICK GAGE

In fact, most urban members are nothing more than customers of Farm Bureau-affiliated insurance companies. The Farm Bureau requires these customers to purchase memberships in order to qualify for low-cost automobile, home, health or life insurance. These members do not necessarily support or even know about the Farm Bureau political activities that membership fees and insurance premiums are bankrolling. Chicago banker Sallyann Garner, for example, became a Farm Bureau member when she took out an insurance policy in 1991.

Garner says she knew that a membership in the DuPage County, Illinois, Farm Bureau came with her policy, but she did not realize that all county members automatically become members of the national organization. Garner learned last April about AFBF's lawsuit to force removal of the Yellowstone wolves. "Wolf recovery happens to be one of my pet programs," she says. "I was extremely upset. I was appalled that I was forced to be a member of the American Farm Bureau just because of my insurance. I ought to be able to choose insurance based on the cost and the value and not unwittingly be part of a political action group that advocates policies I personally object to." A letter to DuPage County Farm Bureau president Michael Ashby brought a response saying that if Garner objected to the policy on "Wildlife Pest and Predator Control" she could vote with her checkbook and find other insurance.

> he AFBF works closely with more than a dozen wise-use groups, including several coalitions that are seeking to eviscerate the Endangered Species Act and lower clean air and water standards.

Ask any Farm Bureau official at the county, state or national level how many actual farmers belong to the organization and it is likely you will not get a straight answer. "We feel like we represent eight out of ten American farmers," says Dick Newpher, executive director of AFBF's Washington, D.C., office. But in fact, Newpher says he has no idea whether that statement is true because AFBF does not keep a central membership list that identifies who is a farmer and who is not. AFBF bylaws clearly spell out two categories of membership, however: voting members who are actively engaged in agriculture or retired from farming and associate members who are not farmers. Newpher says county and state farm bureaus keep separate records for the two member classes, but queries to several state farm bureaus did not produce answers, either. Texas Farm Bureau spokesman Gene Hall says TXFB membership records make no distinction.

Because AFBF is a nonprofit organization (although some state affiliates have set up for-profit companies) it pays no taxes on income from membership dues. In 1993, the Internal Revenue Service ruled that dues from nonfarming associate members – the customers of Farm Bureau insurance companies and other businesses – should be taxed as business income. An IRS survey of these associate members had found that only five percent joined AFBF because of an interest in agriculture. The IRS ruling could have cost AFBF an estimated $32 million in taxes each year. But a group of members of Congress led by Representative David Camp (R-Michigan) came to the rescue. Legislation reversing the IRS decision won approval in 1996 as part of the tax-relief package under House Speaker Newt Gingrich's "Contract With America." During 1995 and 1996, political action committees affiliated with state farm bureaus contributed $109,824 to many of the 126 sponsors and cosponsors of the Tax Fairness for Agriculture Act – including $16,480 to Camp.

In recent years, AFBF and its state affiliates have developed cozy alliances with other conservative political groups, including many of the so-called wise-use organizations. AFBF works closely with more than a dozen of these groups, including several coalitions that are seeking to eviscerate the Endangered Species Act, roll back wetlands protections, lower clean air and water standards and thwart efforts to reduce global warming.

Although these issues may have some bearing on agriculture, AFBF also uses its considerable clout to push policies that have no apparent connection to farming. For example, the Montana Farm Bureau (MTFB) lobbied to require that schools teach creationism on an equal basis with evolution. MTFB also wanted the state to ship convicted criminals to

BRAD MARKEL/GAMMA LIAISON NETWORK

Farm Bureau head Dean Kleckner, right, meets in 1991 with President Bush and Edward Madigan, then Secretary of Agriculture.

Joel Sartore

Critics of the Endangered Species Act and wolf reintroduction demonstrate in connection with a 1994 U.S. Senate hearing in Ronan, Montana. A witness for the Montana Farm Bureau Federation said wolves were of concern to many MFBF members.

Mexico and promoted a resolution urging the United States to withdraw from the United Nations. AFBF's 1998 policy book calls for repeal of the nation's basic civil rights law, the Voting Rights Act of 1965, and restoration of provisions in the 1872 Mining Act "that guarantee the rights and freedom of prospectors and miners." This law has allowed multinational corporations to extract billions of dollars in precious metals from public lands without paying royalties to the U.S. government. It contains no requirements for land reclamation and elevates mining above all other interests on public land, including wildlife habitat and clean water.

Newpher paints a far more benign picture of the Farm Bureau's agenda. "We are probably the least selfish occupational group that there is in America," he boasts. "I don't see us taking strong legislative positions where we set out to be of harm to other parts of our society. I don't think we take extreme positions that hurt other people. We try not to."

The Texas Farm Bureau apparently is not with the program. TXFB pushed for repeal of the federal minimum wage and wanted the government to cut food stamps for poor families whose children also got free lunches at school. When the Texas Agriculture Department adopted regulations to prevent growers from spraying pesticides while farm workers were in the fields, TXFB nearly succeeded in getting the state legislature to revoke those rules. "The new regs weren't anything major that would be a substantial disruption or expense to employers, but you should have heard the screaming and howling. You would have thought somebody had burned their barns and run off their stock," says Texas Rural Legal Aid attorney David Hall, who has represented farm workers injured by pesticides. Both TXFB and AFBF advocate eliminating the Legal Services Corporation, a federally funded organization that provides legal-aid attorneys like Hall for low-income clients.

In North Carolina in 1983, the Farm Bureau opposed a proposal for increased penalties against individuals who hold workers in involuntary servitude – in other words, people who keep slaves. Ten people had been convicted on slavery charges in North Carolina during the previous three years. And in Ohio, the Farm Bureau worked to retain a National Labor Relations Act exemption for large corporate farms. Because of this exemption, workers at egg farms with millions of laying hens have no protection from firing or harassment by their bosses if they try to organize labor unions.

It should come as no surprise that the Farm Bureau defends big agribusiness. The Farm Bureau itself is in big agribusiness. Growmark, a Farm Bureau-controlled grain-marketing cooperative, chalked up $1.57 billion in sales last year. In 1985, Growmark merged its grain terminal operations with agricultural giant Archer Daniels Midland (ADM). ADM took over management of the terminals, and Growmark received ADM stock in exchange. Other Farm Bureau companies own stock in big agribusiness. And if those big agribusinesses prosper, Farm Bureau affiliate stock portfolios stand to reap some of the benefits.

The Farm Bureau also uses its lobbying clout to take care of its other financial partners. Seemingly odd policy positions are easier to understand in the light of the Farm Bureau's insurance and other business interests. For instance, AFBF lobbied against important health-care legislation, including a bill guaranteeing minimum hospital stays for new mothers. State farm bureaus have lobbied hard for limits on medical malpractice damage awards, and AFBF is pushing for privatization of Social Security. It is a far stretch to relate those issues to agriculture, but they certainly affect Farm Bureau financial interests.

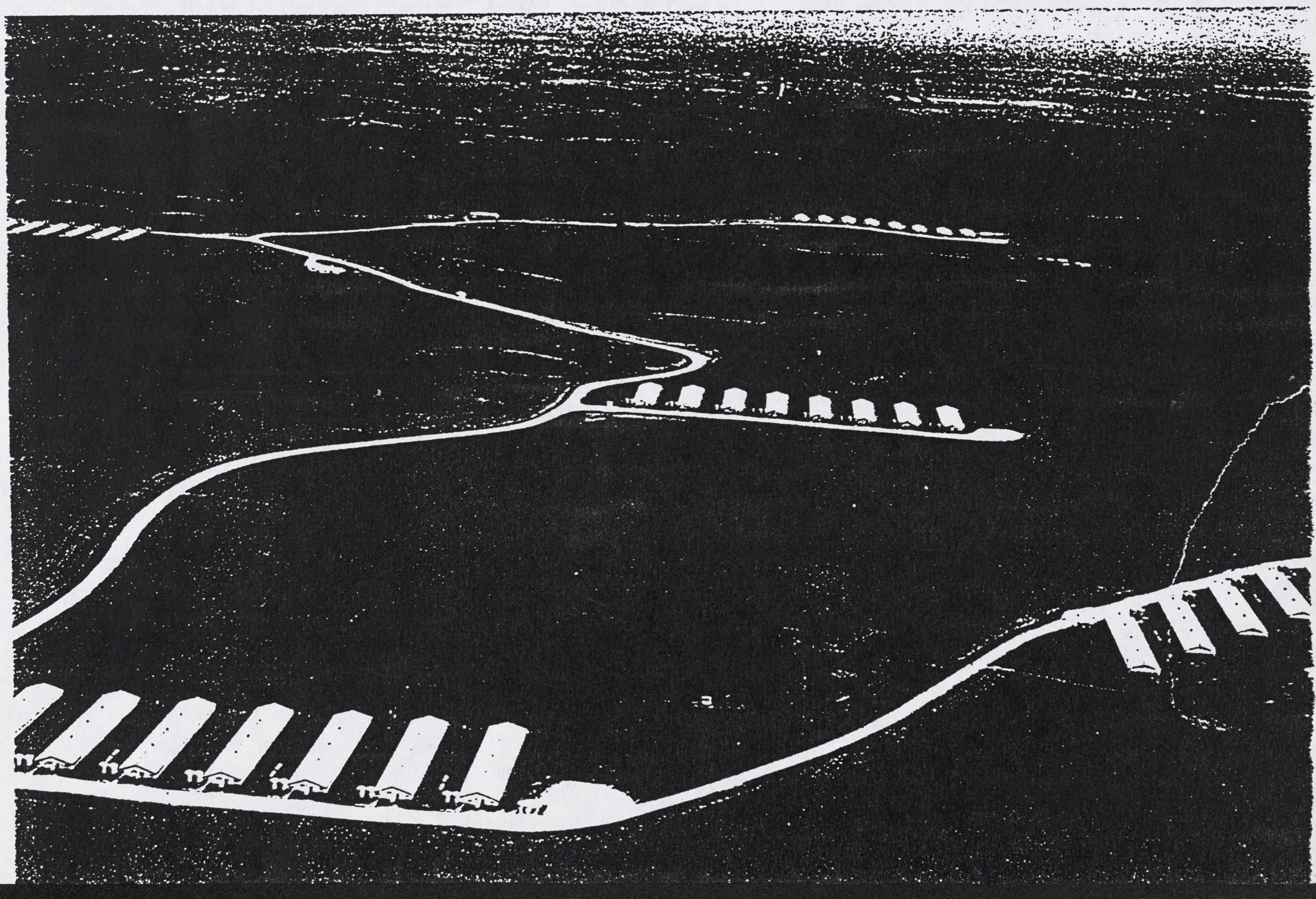
Another example: AFBF is a member of the Coalition for Vehicle Choice, a group that helped defeat legislation that would have raised fuel-efficiency standards for automobiles. FBL Financial Group, which controls Farm Bureau insurance affiliates in 12 states, also owns stock in Ford Motor Company, Texaco and other oil and gas producers, according to FBL financial reports. The Iowa Farm Bureau owns 63 percent of FBL.

"If these people lose their prestige as the spokesmen for agriculture, they're just another insurance lobby, and insurance lobbies are a dime a dozen," Missouri farmer Scott Dye says. "That's why they don't like to talk about how many of those members are actually farmers." Dye's family has farmed in Missouri for 118 years. He has never belonged to the Farm Bureau and says he never will. "They've sold me up the river as far as I'm concerned," he says.

Two Missouri controversies illustrate how out of step the Farm Bureau can be with family farmers. Dye and other small farmers in a three-county area in northern Missouri have been locked in what is so far a losing battle over the presence of concentrated animal feeding operations. These megafarms house as many as 140,000 animals. Rolf Cristen's 600-acre farm is sandwiched between two of these operations. "It stinks at our house continuously," he says. People who have worked around livestock all their lives say they sometimes wake up in the middle of the night and vomit because the stench is so bad.

In the 1980s, Missouri's Air Conservation Commission exempted farms from laws that require other businesses to keep smells under control. Missouri Attorney General Jay Nixon has petitioned the commission to revoke the odor exemption for the largest livestock producers. Fewer than a dozen huge corporate farms would be affected. The exemption for family farmers would not change. Nevertheless, the Missouri Farm Bureau has attacked the proposal, arguing that the odor regulations were not based on sound science and would trample private property rights. Missouri Farm Bureau spokesman Estil Fretwell says the bureau worries that if regulations are imposed on the biggest farmers, they will soon trickle down to

Premium Standard Foods successfully sued Lincoln Township, Missouri, to nullify zoning rules adopted to bar this hog farm.



family farms. "I think we've been very clearly on the side of concerns of the average farmer in the state," he says.

AFBF has made property rights a national priority. The federation wants the federal government to compensate farmers or others who lose money or have to spend it in order to comply with environmental regulations. "When society makes such demands, it is only fair that society share in the cost," reads an AFBF release. At first blush, that policy may sound entirely reasonable, but that is not how the property-rights issue played out in Lincoln Township, Missouri. Before Premium Standard Foods built an 80,000-hog farm outside the town, community leaders tried to keep the corporate farm away by adopting new zoning ordinances. Premium Standard sued Lincoln Township for $7.9 million, alleging violations of property rights. The property-rights issue was never settled – a state court ruled that the township had no zoning authority to begin with, so the hogs moved in.

Environmentalists fear that this kind of thing will occur more often if Farm Bureau-sponsored policies become law. "The hog issue is a perfect example of how this ideology can cause obvious and direct damage to rural residents, including Farm Bureau members," says Ken Cook of the Environmental Working Group, a research and advocacy group based in Washington, D.C. "Does the Farm Bureau seriously mean that communities should pay corporations when towns adopt regulations to protect themselves?" he asks.

"Property rights stop at your fence line," Scott Dye adds. "Just because you call yourself a farmer doesn't give you any right to fog out your neighbor with the stink of hog manure and doesn't give you any right to pollute the water. Believe me, you get a snout full of 80,000 hogs and it will clarify your thought processes real quick."

AFBF President Dean Kleckner owns a hog farm himself, and at the national level AFBF is fighting EPA's current initiative to tighten Clean Water Act regulations on large animal-feeding operations. The Maryland and Virginia farm bureaus have worked to defeat manure-control legislation even though scientists suspect that manure drainage into streams may be contributing to outbreaks of *Pfiesteria piscicida*, a highly toxic microbe that can kill fish and sicken people. Although AFBF says it is trying to protect small farmers from burdensome regulations, Dye says his experience suggests that farmers really have nothing to fear. "There's never been a farmer put out of business by environmental laws," he declares. "They're put out of business by factory farms that skew markets and deflate prices. We've lost 5,000 independent swine producers in Missouri in the last five years – family farms – and they're gone forever. The Farm Bureau has stood on the sidelines and let that happen."

t a Fish and Wildlife Service hearing in Bethany, Missouri, last January, farmer after farmer got up to say that the Farm Bureau did not speak for the farmer.

DILIP VISHWANAT

Missourian Scott Dye, whose farm is near the Premium Standard Foods hog farm, is a strong critic of the American Farm Bureau.

Dye's friend Rolf Cristen has been active in the Sullivan County Farm Bureau for the last decade. Cristen says he firmly believes in the bureau's mission and in working to influence its policies from the inside. The Farm Bureau has so much clout in Missouri, he says, that it is important to have the bureau on your side. On the hog issue, however, Cristen has been getting more help lately from the Sierra Club. "If you would have told me six years ago that I would have a meeting with the Sierra Club, I would have said you are totally off your rocker."

"I would suspect this is causing some concern for the Farm Bureau," the Sierra Club's Ken Midkiff says. "When family farmers start aligning with the Sierra Club, that should be sending up some kind of signal."

At a U.S. Fish and Wildlife Service hearing in Bethany, Missouri, last January, Farm Bureau lobbyist Dan Cassidy showed up to testify against a proposal to add the Topeka shiner to the endangered species list. This minnow can live only in cool, clear-running streams and cannot tolerate pollution. Listing the Topeka shiner could require farmers to take special care to keep sediments and pollutants out of the water.

The Farm Bureau had alerted its members to the hearing, and dozens of farmers showed up. "Cassidy had this big old Cheshire-cat grin on his face when he saw all of these farmers come filing into the room," recalls another man who was there. Cassidy testified first, arguing against the listing. But then farmer after farmer got up to say that the Farm Bureau did not speak for the farmer. According to a head count taken by the Sierra Club, 69 of 87 people present disagreed with Cassidy and supported listing the shiner. Nearly all of those at the meeting were farmers and rural people.

Martha Stevens, who has farmed for 45 years and is nearing retirement, says she is proud that Topeka shiners still survive in northern Missouri streams. "It means we've been doing something right," she says. "If the water kills the fish, it can't be good for us. The Topeka shiner is a darn good indication of when your water is polluted, and I believe we ought to be able to coexist and not pollute to the point that it destroys them and eventually destroys us." Stevens and her husband dropped their Farm Bureau membership a decade ago. "It's been our feeling that they do not represent the grassroots people," she says.

Over the years, the Farm Bureau has regularly opposed plans to benefit wildlife, regardless of the impact on agriculture. AFBF was instrumental in keeping the U.S. Senate from ratifying the global biodiversity treaty approved in Rio de Janeiro in 1992. As a result, the United States remains the only major nation in the world that has not done so. The Idaho Farm Bureau opposed designation of the Snake River Birds of Prey National Conservation Area, which protects habitat of the densest concentration of raptors in North America. The Wyoming Farm Bureau staked out a position against reintroduction of endangered black-footed ferrets.

AFBF lobbyist Jon Doggett acknowledges that the Farm Bureau was instrumental in reversing a funding cut for the U.S. Department of Agriculture's Wildlife Services (formerly called Animal Damage Control), whose agents kill predators on behalf of ranchers. The House of Representatives voted in June to cut $10 million from the Wildlife Services appropriation. The next day, after heavy lobbying by Farm Bureau representatives in several states, the House reversed its decision.

ow that a few wolves are back in the Southwest, the Farm Bureau is arguing that they pose an unreasonable threat. So far, however, most of the danger has been to the wolves.

In the Southwest in the last five years, Wildlife Services has killed or trapped mountain lions, black bears, coyotes and foxes even in designated federal wilderness areas, including the Santa Teresa Wilderness in Arizona and the Apache Kid Wilderness in New Mexico. Ranchers had complained that these predators had attacked their calves. "You'd think if there was one place that should be predator-friendly it would be the wilderness," says John Horning of Forest Guardians. "It boggles the mind that on the cusp of the 21st century we are paying federal employees to kill predators on federal land for the benefit of a handful of people."

By the 1970s, government agents and ranchers had wiped out the Southwest's wolves. Now that a few are back, the Farm Bureau is arguing that they pose an unreasonable threat. So far, however, most of the danger has been to the wolves. Last April, a Tucson man who had set up camp within a mile of where a group of wolves had been released shot and killed a male. According to news accounts, the camper at first said he shot the wolf because it had attacked his dog (the dog recovered and is doing fine), then changed his story, saying he shot because the wolf had come within 50 feet of his wife and children. FWS decided not to prosecute.

The wolves are getting blamed for more than frightening campers. To hear Farm Bureau officials tell it, these predators will destroy the ranching economy. "Our membership really wonders why the federal government is spending millions of dollars putting predators into rural areas where farm and ranch families are having a real difficult time hanging on to the family ranch," says AFBF lobbyist Jon Doggett.

Although Defenders of Wildlife in the last decade has paid ranchers some $60,000 for livestock losses to wolves, Doggett says ranchers do not believe they can always prove, or even know for sure, that a calf has been killed by a wolf. But according to Defenders' Northern Rockies Representative Hank Fischer, determining whether livestock has been killed by wolves is not difficult. "Wolf kills are way down on the list of things that harm livestock, way below being struck by lightning or hit by automobiles," Fischer says. "We are talking about a small level of predation, and if that's enough to tip the livestock industry over the edge, it has a pretty uncertain future anyway."

Other factors are playing a much more important role in the troubles of cattle country. These days, people are eating less beef. A lot of ranch land has been damaged by overgrazing and other abuse and cannot sustain as many cattle as in the past. On top of that, the beef market is controlled by near-monopolies. Ranchers are in trouble, says Rocky Mountain Farmers Union President Dave Carter, but not because of wolves. "We do have some concerns about the wolf reintroduction, but on the whole we're more concerned about the wolves in the marketplace than the wolves up in Yellowstone," he declares.

The National Farmers Union competes directly with the Farm Bureau but is smaller and takes a much different approach to agricultural and environmental issues. The Farmers Union is heir to an agrarian populist tradition that began around the turn of the century as a fight against usurious banking practices, unscrupulous grain dealers and market speculators. In the 1920s Farm Bureau leaders railed against the "radicalism" of these populists and pledged to work against any policies that might help them.

Some of that old enmity still lingers. Rocky Mountain Farmers Union legislative coordinator Melissa Elliott says she's been disappointed that the Farm Bureau has not helped more with issues that make a real difference in the West. "The market is definitely a bigger problem because every independent producer is affected, and it's literally driving people out of business," Elliott says. "The wolf isn't doing that. Unfortunately we're always on opposite sides of the coin [from the Farm Bureau], and I wish that weren't so. We're all in the same boat. We need to be rowing in the same direction."

Setting up the wolf as the enemy, along with environmental-protection laws and the federal government, diverts attention from more important, and complicated, questions about who controls agriculture in this country and how that control is achieved. But it is just possible that those are questions that the American Farm Bureau Federation does not want asked or answered. □

Vicki Monks, a freelance writer in Santa Fe, New Mexico, reports frequently on wildlife and environmental issues.

Pollution Linked to Feminization of Wild Animals

Fish half male, half female

By Marla Cone
Los Angeles Times

Los Angeles

In a surprising scientific discovery that suggests pollution is feminizing animals throughout the wild, everyday concentrations of sewage effluent in rivers appear to contain estrogenlike chemicals potent enough to cause fish to be born half-male, half-female.

The finding by British scientists provides strong new evidence that hormone-altering pollution — one of the most troubling and controversial environmental issues of modern times — could be a global ecological threat.

Other recent studies had found scattered populations of animals with bizarre sexual defects living in highly polluted waters, but the new research suggests that the problems are more widespread than previously detected.

The British researchers said they uncovered "very compelling evidence" that sewage treatment plants routinely release hormone-like compounds into rivers that are feminizing "a surprisingly large proportion" of wild fish. The fish were found in eight rivers throughout Britain that are considered typical in terms of pollution, so scientists suspect damage to sex hormones is so pervasive that it could be happening in many rivers around the world.

"The incidence and severity of intersexuality ... is both alarming and intriguing," researchers from Brunel University and the British government reported in the September issue of the journal Environmental Science and Technology.

Some male fish have such mixed-up hormones that they are born with ovaries and eggs instead of sperm ducts. In two of the eight rivers downstream of sewage treatment plants, 100 percent of the male fish sampled had feminized reproductive tracts, ranging from severe to slight. The other six rivers had rates from 20 percent to 80 percent.

Hundreds of widely used man-made chemicals — including pesticides, industrial compounds, dioxins and ingredients of plastics and detergents — are believed to mimic estrogen or block testosterone, disrupting the endocrine system that is critical to sexual development.

In their report, the scientists called their findings "the first documented example of a widespread sexual disruption in wild populations of any vertebrate." Hormonal havoc, however, has previously been reported in alligators, birds, river otters, carp and other U.S. wildlife in isolated locations.

The phenomenon of "intersex" animals was first discovered in the 1970s, but it was dismissed as a fluke until the early 1990s, when biologists found feminized alligators in a highly polluted Florida lake and began to suspect that man-made chemicals were altering sex hormones.

The British work "is an extremely important study for many reasons," said Theo Colborn, a World Wildlife Fund scientist and activist who was one of the first to notice a pattern of hormonal problems in animals. The sexual damage the researchers found "is pervasive, it's widespread," Colborn said. "That's what's disturbing about this."

Judith Weis, a Rutgers University marine biologist who studies the impact of pollution, said the British research "lends more support to endocrine disruption as being a very serious issue."

Adult animals are unharmed by hormone-imitating pollutants; instead, the damage is inflicted on the next generation. Mothers pass the excessive amounts of estrogen to their embryos or fetuses, which cannot distinguish between fake estrogens and real ones. When this estrogen boost comes during a critical phase of sexual development, genetic signals go haywire and males are born with feminized genitalia or other reproductive problems.

No one knows what threat, if any, these man-made estrogens pose to human health and fertility.

Some scientists suspect that men exposed in their mother's womb might have depleted sperm counts that lower their fertility; it also might explain a recent surge in testicular cancer.

Hormones play the same vital sexual role in humans as they do in fish and other animals. Although people are exposed through food and water to the same pollutants as water-inhabiting animals, they encounter much lower doses, so any human effects may be subtle.

One of the most surprising aspects of the British findings is that fish are suffering so many sexual defects in a part of the world with sophisticated environmental laws and technologies. Scientists wonder how minute concentrations of fake hormones in the environment — which are hundreds of times less potent than natural estrogen — could have such a severe impact.

Scientists do not know which chemicals are to blame, since sewage is a mix of wastes from homes and industries — everything that is washed down drains.

The culprits could be anything from the urine of women excreting artificial hormones from birth control pills, to pesticides or plastics.

"It's really anybody's guess as to what is causing this," said Weis, who serves on a U.S. Environmental Protection Agency task force developing a national plan to screen chemicals for hormonal effects.

Evidence is emerging that wildlife is being feminized in waters where modern environmental practices and laws are followed and the ecosystem appears outwardly healthy.

The reproductive damage might have dire consequences for an ecosystem, because if males are sterile, an entire animal population might gradually be depleted. Fish, in particular, are an important link in the world's food chain.

So far, the fish in the British study — a species called "roaches" — remain abundant, even in the Aire and Nene rivers, where 100 percent of tested males were feminized. Apparently some of the males still have enough of their systems intact to reproduce.

"What we still don't know is if these intersex fish are reproductive or not. That's the bottom line," Weis said. "Some of them have no sperm ducts, so obviously they can't reproduce."

Because females are more critical to reproduction than males, populations can regenerate themselves even if only a few males are fertile. Over the generations, though, if feminization remains unchecked, fisheries could collapse.

Farmed Fish Replacing the Ocean's Wild Bounty

But growing industry poses threats to sea environment

By Colin Woodard
Chronicle Foreign Service

Bay Bulls, Newfoundland

The cod have come back to this once-productive fishing community — but not in the dense schools that once chased tiny fish into the bay from the cold North Atlantic.

These schools are growing fat in floating pens in which they can be seen circling in search of processed fish feed.

The cod in Bay Bulls may be the ancestors of your next fresh fish meal. Many were grown from eggs by a private aquaculture company and are held as a future brood stock.

Because of the overfishing and collapse of much of the North America's cod populations earlier this decade, Newfoundlanders may soon end up hatching and growing more cod than they can catch out on the once-bountiful Grand Banks.

"Right now, there are very few areas where we still have a commercial fishery," said Brian Meaney of the Newfoundland Ministry of Fisheries. "Farming cod or fattening the smaller fish we still do catch is creating employment and providing a quality product."

Growing Industry

This is the promise of aquaculture — the rapidly growing global industry that breeds and grows an increasing share of the mollusks, shrimp and fish eaten at restaurants and dinner tables worldwide.

Proponents have long argued that aquaculture can reduce fishing pressure on wild stocks and provide new jobs, while helping to feed the world's rapidly growing population.

"Aquaculture is going to grow because there simply will not be a supply of seafood products based on capture fisheries," said Leroy Creswell, an aquaculture research scientist and former president of the World Aquaculture Society.

"Many species are tapped out and in many cases have crashed or are in rapid decline," he added. "Aquaculture is needed to bridge the gap."

AQUACULTURE
Year of the Oceans

Global aquaculture production doubled during the past decade and now accounts for a quarter of the world's food fish supply, according to the Rome-based U.N. Food and Agriculture Organization.

Worldwide, the industry produces an estimated $43 billion worth of cultured fish and aquatic plants — a figure that is expected to continue growing.

Environmental Questions

But as the industry grows, so has the controversy over its environmental effects, particularly in marine waters where fish farming is a relatively new activity. Critics fear that intensive aquaculture operations are stressing seas, estuaries and coastal ecologies that often are already damaged by overfishing, coastal development and pollution.

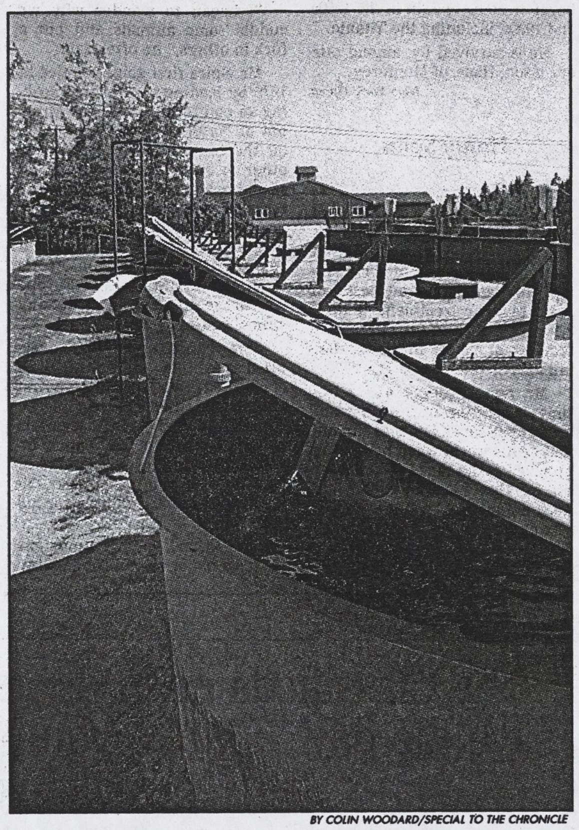
Asian shrimp farms are blamed for the poisoning and destruction of mangrove forests, which are key nursery habitats for many marine creatures. U.S. and Canadian salmon farms are blamed by many for contributing to declines in water quality, wild salmon populations and the deep-sea schooling fish that are caught and ground to feed penned salmon.

"It's an enormous industry, and it's not just going to go away," said Frederick Whoriskey of the Atlantic Salmon Federation, a conservation group based in St. Andrews, New Brunswick. "We need to find solutions so that salmon farms clean up their act and function sustainably."

Started in China

Freshwater aquaculture has been around for a long time. It is thought to have started in China about 5,000 years ago with the beginning of carp farming.

Then, as now, the carp ponds were fertilized with animal manure, producing the algae, plankton and plants eaten by the fish. China now accounts for nearly two-thirds of world production. And most of that is carp.



BY COLIN WOODARD/SPECIAL TO THE CHRONICLE

Salmon fry are nurtured in tanks at a hatchery in St. Andrews, New Brunswick, Canada, then transferred to growing cages in the ocean.

Today, aquaculture is becoming as diverse as conventional agriculture.

Seaweed is harvested from Japan to California for industry, fertilizer and food. In some parts of the United States, clam diggers plant sprat on their mud flats and collect them when they have grown, while oyster and scallop banks are often enhanced by planting hatchery-grown sprat. Cod, halibut and sturgeon may soon join salmon in coastal growing cages.

The vast majority of the world aquaculture industry farms with little harm to the environment.

Freshwater carp, catfish and tilapia are plant-eaters and are usually raised in special ponds where they help convert potentially harmful organic wastes into edible fish meat. Shellfish like mussels, scallops and oysters filter algae and plankton from seawater, so farmers don't pump feed or medicine into the environment.

Destructive Species

But the farming of other species — particularly shrimp and salmon — can be extremely destructive.

Salmon, a carnivorous species, are grown in cages floating in coves and bays where they are fed processed fish meal made from other fish. Uneaten feed, fish wastes and antibiotics drift from the crowded cages and are blamed for deterioration of water quality and bottom habitat and for outbreaks of disease in wild fish populations.

And because farmed salmon and shrimp (normally a scavenger) are fed meals and oils made from small, edible schooling fish like mackerel, capelin, sardines and anchovies, the farms are net consumers rather than producers of fish protein.

"By taking these fish out of the ocean to feed to farmed fish, we're undermining the integrity of the marine food web," said Rebecca Goldburg, a staff scientist at the Environmental Defense Fund in New York.

"On land, we grow herbivores like chicken and cattle because it's an efficient way to make protein," she added. "It makes no more sense to grow carnivores in fish farms than it does to grow tigers on land."

Biological Pollution

Goldburg's organization is also concerned about biological pollution. Farmed salmon frequently escape from sea cages, sometimes in large numbers, and they can pass on diseases and unfavorable genetic traits to wild salmon.

A study by Whoriskey and three other scientists found evidence that farmed salmon were not only spawning in a local river, they may now account for as much as 55 percent of the eggs there. Wild salmon are extremely vulnerable; this year, estimated wild Atlantic salmon populations reached their lowest level on record, according to the Atlantic Salmon Federation.

In April, an outbreak of infectious salmon anemia forced New Brunswick farmers to kill 1.2 million fish. The previous month in British Columbia, members of the T'Sou-ke native American nation arrived in war canoes to protest salmon farming that they say is destroying their traditional fishing grounds.

Aquaculture proponents admit that salmon farms have had negative effects, particularly when overcrowding is allowed. But they say these problems must be understood in the proper context.

"It's in the industry's own best interests to maintain the best possible environmental quality — the fish depend on that," said Jay Parsons, a researcher at the Memorial University of Newfoundland and the former president of the Aquaculture Association of Canada.

Other Sources of Pollution

They point out that the environmental impact of salmon or shrimp is far less than that of other industries that pollute the marine environment.

"Paper mills, oil spills and municipal sewage all pollute the environment," Parsons said. "I'm not saying there aren't problems, but there are a lot of other things we should be concerned about that have a far greater impact than salmon aquaculture ever will."

Under pressure from regulators and sport fishermen, the industry is reportedly working on plant-based feed products and improved husbandry practices that reduce the risk of disease and pollution. Switching to closed-loop farms on land is an option that would reduce the impact of salmon farms by monitoring and treating waste water before it is released.

"Most people involved in aquaculture have a strong commitment to creating responsible, sustainable industry," said Creswell. "But we can't do things with zero impact, any more than you can drive a car to work or raise poultry without affecting the environment.

"Aquaculture is agriculture; it just happens to be done in the water," he said. "Terrestrial agriculture got thousands of years to perfect itself; in the sea, we're having to do it in a few decades."

Chronicle correspondent Colin Woodard is writing a series of articles on the global marine environment, inspired by the United Nations' designation of 1998 as the Year of the Oceans.

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M-F(PM), Sat(AM); 6,308

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What is a species? Question goes beyond word

By ROBERT BEHNKE
CSU Fishery Biology

What is a species? A species is a species is a species, stupid! Such a response might be expected for such a question. Species is one of those elusive words that everyone understands, but can't clearly define the meaning.

Lack of precise definition is understandable because among the experts who study the classification of plants and animals, called taxonomists, considerable disagreement exists on what species are and how species should be defined.

The implications of the meaning of species goes much beyond playing word games. It is basic for proper implementation of the Endangered Species Act.

The act now is up for re-authorization by Congress and among the many points of contention, the definition of "species," what should be eligible for protection, is a major focus of debate. Congress instructed the National Academy of Sciences to appoint a committee to write a definition of species for the act.

All of us should be concerned about how "species" is ultimately defined. This definition will guide how the act can be applied and will impact future development and natural-resource management nationwide.

The goal of the act is to prevent or reduce the rate of extinctions and preserve biodiversity. Biodiversity consists of diversity among species, which is called interspecific diversity, and diversity within a species which is intraspecific diversity.

It is intraspecific diversity, meaning a segment of a species, that is the point of contention for defining what is now protected under the act. Thus, a small part of a species can be listed for protection under the act even if the species as a whole is widespread and abundant.

This has been done for populations of chinook salmon and sockeye salmon. Such listings raise the question of how fine can the line be drawn. Would a population of squirrels in a city park isolated by urban sprawl from neighboring squirrel populations, be eligible for listing?

The federal agencies responsible for implementing the act, the U.S. Fish and Wildlife Service and the National Marine Fisheries Service have recognized the futility of defining "species" for the act and instead developed a concept called Evolutionary Significant Unit as a way to implement the intent of the act. These agencies look for ways to quantify the significance of a particular part of a species' contribution to the diversity of that species as a whole.

I have studied at Colorado State University for many years the evolution of trout species and subtionary significant — the type of diversity most desirable to preserve — focuses most on the replacibility of a given species or specific part of a species. If a particular population became extinct, to what extent might it be replaced by another unit of the species?

For example, if a population of squirrels was lost from a city park, it could be fully replaced by introduction of squirrels from neighboring populations. They would not qualify for listing under the act.

However, the sockeye salmon of Redfish Lake, Idaho, is another matter. The sockeye salmon of Redfish Lake are the most inland population in the world of this species. The fish are located more than 900 miles from the ocean. The life history and physiological adaptations necessary for these fish to survive so far inland makes it highly unlikely that any of the sockeye salmon populations along the Pacific Coast could replace the Redfish Lake sockeye if it became extinct.

Thus, it qualifies as a significant evolutionary unit because it cannot be fully replaced by any other form of the species.

It is this irreplaceable type of intraspecific adaptations that should be accounted for in any modified definition of species for the re-authorization of the Endangered Species Act. Let's hope Congress asks some hard questions about the definition of species in relation to how the act will be revised before approving any final changes.

— Robert Behnke is a authority on the classificat salmonid fishes, the auth many scientific papers translator of Russian fisher erature into English.

Species in a Bucket

For a few frightening moments, there was only myself standing between life and extinction

by Edwin Philip Pister

[The naturalist] looks upon every species of animal and plant now living as the individual letters which go to make up one of the volumes of our earth's history; and, as a few lost letters may make a sentence unintelligible, so the extinction of the numerous forms of life which the progress of cultivation invariably entails will necessarily render obscure this invaluable record of the past. It is, therefore, an important object [to preserve them].... If this is not done, future ages will certainly look back upon us as a people so immersed in the pursuit of wealth as to be blind to higher considerations.

Alfred Russel Wallace
Journal of the Royal Geographical Society (1863)

When I retired in 1990, I built a small office in my backyard, equipped it with a phone and word processor, and began to reflect seriously upon a career that began in 1951 and continues even in retirement. I remain keenly aware of the legendary biologist Aldo Leopold's admonition that one of the penalties of an ecological education is that one lives alone in a world of wounds.

Virtually my entire career was spent as a district fishery biologist for the California Department of Fish and Game in the state's vast eastern sierra and desert regions. I worked on a great variety of management and research programs—from trying to keep millions of sports fishermen supplied with trout to preserving the biological integrity of desert springs that support life forms totally unknown to most Americans and even to most scientists.

Having studied wildlife conservation at Berkeley in 1948 under the tutelage of Aldo Leopold's son, A. Starker Leopold, I was exposed to the Leopolds' passionately held values regarding the natural world. Impressed by their view that nonconformity is the highest evolutionary attainment of social animals, I carefully avoided the usual career track that would have landed me in one of my department's major offices in a big city. As a graduate student, I had specialized in limnology, the study of freshwater lakes, and was given the responsibility for nearly a thousand bodies of water extending from the crest of the Sierra Nevada eastward to the Nevada state line. I was especially intrigued by the diversity of the landscape in my charge; if I left the roadhead near the base of 14,494-foot Mount Whitney at 9:00 A.M., I could make a leisurely drive to the east and have my lunch 282 feet below sea level on the floor of Death Valley. This area's life forms are commensurately diverse.

Today I sit at my desk surrounded by forty little pocket diaries, each one summarizing a year of my career. So many memories and experiences are packed into these 2.5- by 4-inch volumes, which, together, fill less than a shoe box. Daily entries recall a multitude of experiences: scaling through the usual routine meetings, conducting a twenty-seven-year project to restore the California golden trout within the Golden Trout Wilderness (still in progress), fighting scores of ill-considered and highly destructive entrepreneurial invasions of valuable habitats and recreation areas, managing a legendary reservoir fishery where success is measured by tons of trout harvested, then moving 180 degrees from consumption to conservation by helping save the Devil's Hole pupfish (*Cyprinodon diabolis*), a battle carried successfully to the U.S. Supreme Court.

In 1976, the Court's landmark decision protected Devil's Hole—a swimming-pool-sized window into the underground aquifer and a disjunct portion of Death Valley National Monument—and its dependent life forms from the impact of a nearby ranching operation. (The ranchers were consuming vast quantities of unreplenishable groundwater from an aquifer that had been undisturbed since the Pleistocene.) The smallest and most highly evolved of the Death Valley system pupfishes, the Devil's Hole pupfish has been isolated from nearby pupfish populations for approximately 44,000 years. It exists in probably the most confined habitat of any vertebrate animal in the world: the ten- by fifty-foot pool in which it has evolved since its isolation.

Of more than ten thousand entries contained in my diaries, the date August 18, 1969, stands alone as the most dramatic and meaningful. Written with naïve understatement: "Transplanted *Cyprinodon* at Fish Slough; purchased alkaline D-cells, \$2.00," this cryptic entry summarized a series of events that, had they not gone right, would have accompanied the greatest tragedy of my career. As it turned out, what happened that day simply underscored the lessons I had learned earlier from the Leopolds and other ecological mentors. Perhaps such an experience was necessary for me to fully comprehend that a person's values, which serve as a compass in uncertain times, are in the long run vastly more important than the sport-fishing technologies that have often created more problems than they have solved.

During the several pluvial periods of the Pleistocene epoch, much of the Great Basin of the American West was covered by large, freshwater lakes. With the approach of the Holocene, these waters shrank and largely disappeared, and fishes were isolated within the few remaining permanent aquatic habitats. In North America, only the Cuatro Ciénegas of Coahuila, México, have as many well-de-

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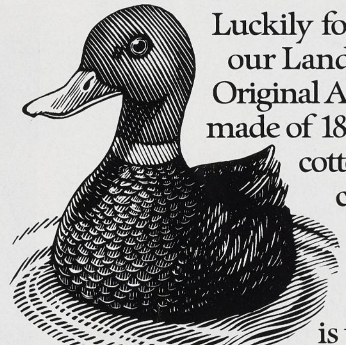

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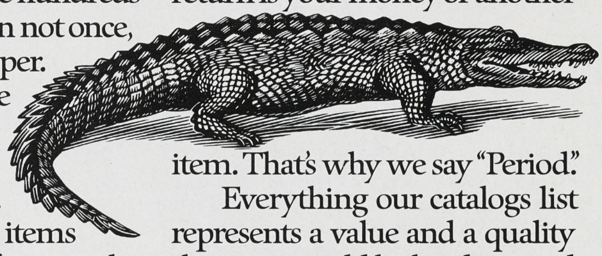

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fined local populations (species confined to the very small, isolated habitats in which they evolved). The Death Valley drainage area of eastern California and western Nevada is comparable to Charles Darwin's Galápagos Islands and their finch populations. They constitute, in effect, islands of water in a sea of sand.

One such habitat exists in eastern California's Owens Valley, where the Owens pupfish (*C. radiosus)* has been evolving since the Pleistocene. Because of major habitat changes and the introduction of predacious gamefishes (a deadly combination) during the early part of the twentieth century, the Owens pupfish was gradually eliminated from a range that once covered vast marshlands. By the time it was scientifically described in 1948, the species was believed to be extinct. One of the Death Valley area pupfishes, all of which evolved in the absence of predatory fishes, the Owens is almost totally defenseless against such introduced predators as largemouth bass, which I call "chainsaws with fins." The Owens pupfish was among the first fishes to be designated an endangered species, a status that it unfortunately still retains.

Pupfishes (named for their frolicsome, playful behavior) are members of the killifish family, a group of fishes very popular among aquarium enthusiasts. The Owens pupfish is the largest of the nine Death Valley pupfishes, occasionally reaching two inches in length; the Devil's Hole pupfish rarely exceeds one inch. Habitats are varied. The Owens pupfish thrives in the shallow, warm water that hot summer days bring to desert marshes; this same habitat may be covered with an inch or two of ice during wintertime, when air temperatures drop below zero. Conversely, the Devil's Hole pupfish lives in the upper reaches of a cavern so vast that its depth has never been determined, and in water at a constant 92° F. All pupfishes are feeding opportunists, consuming immature insects and algae. They are also highly territorial.

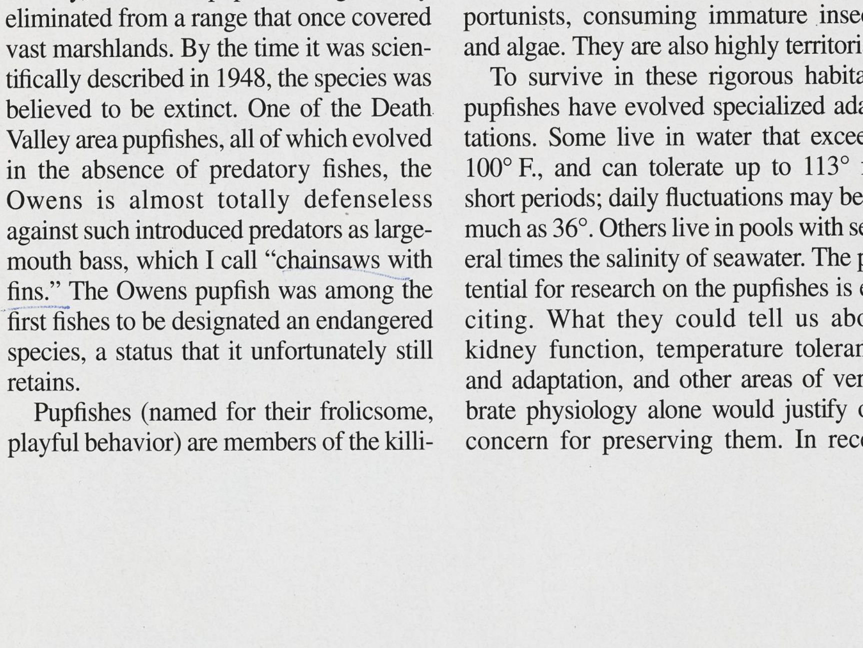
To survive in these rigorous habitats, pupfishes have evolved specialized adaptations. Some live in water that exceeds 100° F., and can tolerate up to 113° for short periods; daily fluctuations may be as much as 36°. Others live in pools with several times the salinity of seawater. The potential for research on the pupfishes is exciting. What they could tell us about kidney function, temperature tolerance and adaptation, and other areas of vertebrate physiology alone would justify our concern for preserving them. In recent years, however, it has been heartening to note a shift in emphasis from what they can do for us to what we can do for them, regardless of their potential value.

In 1964 researchers located a remnant population of Owens pupfish in a desert marshland called Fish Slough, a few miles from my home in Bishop, California. A recovery effort was started by gradually reintroducing them into a few apparently suitable habitats, thereby getting a jump on the more sophisticated recovery programs made possible later under the Endangered Species Act of 1973. These early preservation efforts for fishes preceded the relatively recent, and highly commendable, formalization of the science of conservation biology.

However, an unusual set of circumstances that began to coalesce in the late 1960s brought the Owens pupfish to the brink of extinction. Without constant surveillance, which even now is very difficult for harried state biologists to maintain, the pupfish gradually disappeared from their new homes and finally were confined to a room-sized pond a short distance below Fish Slough's northwest headwater springs. The winter of 1968–69 had brought heavy rains to the Owens Valley, but by August the unusually thick vegetation was throwing off a great deal of moisture, and an unexplained reduction in spring flow contributed to the rapid depletion of the pond. It was almost completely dried up when an alert assistant came into my office and announced: "Phil, if we don't get out to Fish Slough immediately, we are going to lose the species." His pronouncement was no exaggeration. It was the hard truth!

I stopped work on a trout management program for a major reservoir (the relative importance of the two projects has long since served as a source of humor for me), shouted a few words of explanation to our receptionist, and bolted for the door. Grabbing buckets, dip nets, and aerators, we were joined by another colleague and immediately headed for Fish Slough, normally a fifteen-minute drive north of our office in Bishop (we shaved at least five minutes off the usual driving time.) We hastened to the drying pond and carefully removed 800 remaining individuals, placing them in three wire mesh cages within the main northwest channel of the slough, in a diminishing flow already less than two cubic feet per second. We planned to move them later to safer locations within the same general area.

Having done all we could for the mo-



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Roots Research subscribes to the Direct Marketing Assn. Guidelines for Ethical Practices ment, we decided to take a quick dinner break before returning to move half of the fish (about 400) across the slough to a location supplied by another spring source. In endangered species preservation work, a cardinal rule is always to place your eggs in more than one basket. We had come very close to witnessing a species extinction or, nearly as bad, a population so reduced in numbers as to eventually effect the same tragic consequence.

Temporarily alone in the marsh, I decided to make one final check (sometimes it pays to be a worrier). A glance into the nearest mesh cage showed that we were not yet out of the woods. In our haste to rescue the fish, we had unwisely placed the cages in eddies away from the influence of the main current. Reduced water velocity and accompanying low dissolved oxygen were rapidly taking their toll. When taken from their natural habitat, pupfish are fragile creatures. They were overcrowded in their cages and had been stressed by unavoidably rough treatment on a hot summer afternoon.

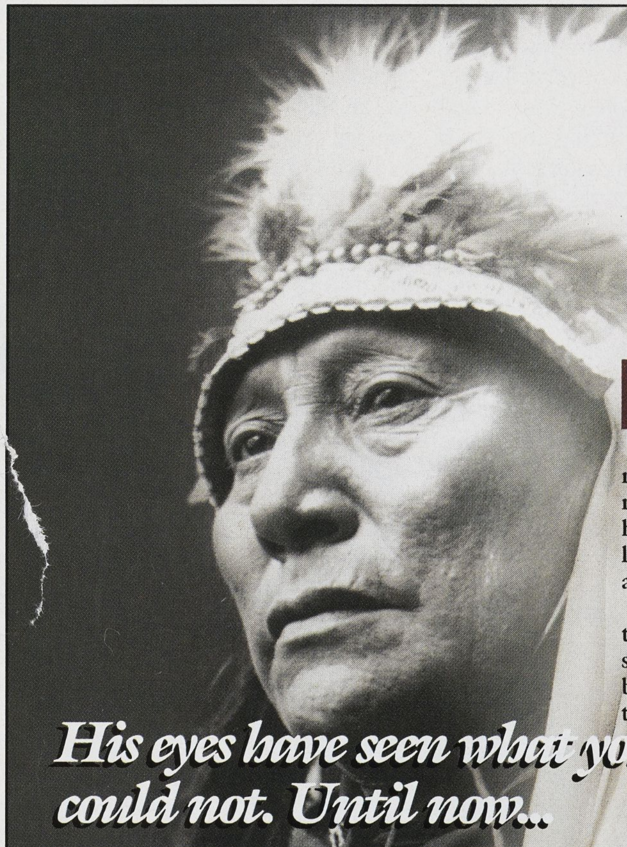
A number of dead and dying fish were already floating belly up or swimming irregularly, and it was clear that both mesh cages and fish would have to be moved immediately upstream to more favorable conditions nearer the springheads. I ran to my pickup truck and found only two buckets (the other two were on their way back to town). However, there were two aerators available in addition to the all-important dip net.

I netted the surviving fish into the buckets, wincing as each dead one forcefully demonstrated the fragility of life. I then relocated the cages and returned to the buckets, trusting that the battery-powered aerators had not failed during my brief absence. Although the passage of time has obscured my exact words and thoughts as I lugged two heavy buckets and their precious cargo (each weighing more than thirty pounds) over the treacherous marsh terrain, I remember mumbling something like: "Please don't let me stumble. If I drop these buckets we won't have another chance!" I distinctly remember being scared to death. I had walked perhaps fifty yards when I realized that I literally held within my hands the existence of an entire vertebrate species. If I had tripped over a piece of barbed wire or stepped into a rodent burrow, the Owens pupfish would now be extinct! But good fortune smiled upon us, and the recovery continues today.

Efforts to preserve endangered desert life forms never end, but essentially constitute only a temporary reprieve as aquatic habitats gradually decline throughout North America. Indiana University's Lynton Caldwell, speaking of our environmental crisis, observed that while endangered species are part of this lamentable phenomenon, "more importantly, the crisis is concerned with the kind of creatures we are and what we must become in order to survive."

We have received adequate warning from our prophets. Aldo Leopold's "Land Ethic," published more than forty years ago in *A Sand County Almanac,* redefined Gifford Pinchot's "resource conservation ethic" (the greatest good for the greatest number in the long run) and placed humans as simply another species within the global ecosystem. This concept has since become painfully obvious as we learn more about ourselves in relation to our environment.

Having spent much of the past two decades responding to the cynical question: "What good are they?" (in reference to my efforts on behalf of the pupfish and similar "insignificant" organisms), I have made use of an effective counterquery: "What good are *you*?" (a very thoughtful question). I then add a Leopold corollary: "To keep every cog and wheel is the first



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precaution of intelligent tinkering."

Rank-and-file American citizens have been generally apathetic about the conservation of biological diversity, but one would hope not to find similar unconcern within the scientific community. Yet there is much complacency among professionals, particularly among those biologists trapped within a tenure track and faculty advancement syndrome that often ranks quantity over quality in the research endeavor. If such scientists express an interest in conservation, they usually are of the opinion (naïvely and incorrectly) that someone else will attend to saving species. At the 1992 annual meeting of the American Society of Ichthyologists and Herpetologists, for instance, only a small percentage of 385 research papers related to the specific area of conservation.

Workers in the pragmatic field of conservation biology frustrated by a critical need for answers to questions posed by species recovery programs, draw analogies of mowing the lawn while the house burns down. The possibility always exists, of course, that *any* research, no matter how seemingly esoteric, may someday be of value in saving a species. Albert Einstein put it this way: "I have little patience with scientists who take a board of wood, look for its thinnest part, and drill a great number of holes where the drilling is easy." Unfortunately, the deadly serious matter of preserving biodiversity generally places one in the position of facing unpredictably thick boards, full of knots, and then being forced to drill holes with a bit significantly dulled by the bureaucratic process.

As I walked back to my truck following the final transplant within Fish Slough, the sun had long ago set. In my dip net remained a few dead pupfish. I glanced up at the darkening desert sky and thought of Pierre Teilhard de Chardin's concept of the infinitely large, the infinitely small, and the infinitely complex, represented here (in order) by the Milky Way, the pupfish, and the difficulty in pointing out the paramount value of such things to an increasingly materialistic society.

The day had been long. We had won an early round in a fight that will inevitably continue as long as we have a habitable planet. As a realist, I could not help but ponder the ultimate fate not only of the Owens pupfish but of all southwestern fishes and species in general. I wondered about our future. Can the values driving the industrialized nations be modified sufficiently to allow for the perpetuation of all species, including humans? Will we ever realize the potential implicit in our specific designation as *Homo sapiens,* the wise species? I hope the day will come when public policy will be guided by the wisdom of Aldo Leopold: "A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise." Such recognition could constitute perhaps the first major step toward creating the sustainable society upon which our long-term survival obviously depends.

That August day twenty-three years ago had been a very humbling experience for me. The principles of biogeography and evolution I had learned many years before at Berkeley had taught me why the pupfish was here; it took the events of those few hours in the desert to teach me why *I* was. Such are the reflections of a biologist who, for a few frightening moments long ago, held an entire species in two buckets, one in either hand, with only himself standing between life and extinction.

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Close Encounters

by Gail S. Cleere

No other planet in the Solar System has elicited more excitement than Mars. Known since antiquity, Mars is easily recognizable by its color—blood red—and this easily explains its association with the gods of war, Nergal in Babylonia, Ares in Greece, and Mars in the vast Roman Empire. This month, the red planet rises in advance of sunset and is well up in the east at the end of evening twilight, near the twin stars Castor and Pollux in the constellation Gemini. Glowing brightly at -1.4 magnitude, Mars is high above the southern horizon about midnight. During the present passage of the earth between Mars and the sun, our planet makes its closest approach to Mars on January 3 (about 58 million miles away). Four days later it reaches opposition, meaning that Mars will be opposite the sun in our sky and therefore up for the entire night, making it a great time to look at this planet.

In earlier times, such a close approach of Mars would have seized the public's imagination. One hundred years ago, it was popularly believed that there was indeed life on Mars. After all, hadn't the Italian astronomer Giovanni Schiaparelli announced in 1877 that he had seen "canals" on Mars? Wasn't this obviously a sign of intelligence? And hadn't our own Percival Lowell confirmed this sighting with many of his own observations right here at home in Flagstaff, Arizona? These canals were assumed to be "stupendous systems of irrigation" bringing water down from the Martian poles to its "centers of population and industry." In 1910, the writer Garrett P. Serviss told us in *Curiosities of the Sky* that "the miraculous feat of engineering" was due to the planet's lower gravity force. Mars has an atmosphere, albeit thin, some water in its icecaps, and a surface temperature that is harsh but does not preclude life entirely. And so obviously, a close approach of the planet was the right time to communicate with our brothers on Mars. Their secrets could be revealed "from their own lips," Serviss wrote, "if we could get into wireless telephonic communication with the Martians."

Mars mania, as astronomer and writer Roger Sinnott calls it, increased during Martian oppositions. In 1898, H. G. Wells penned his classic *The War of the Worlds*. In 1909, there was a plan to spread an army of 5,000 men holding ten-cent shaving mirrors across Texas, ready to flash Mars in an attempt to signal intelligent life there. A wealthy Parisian widow offered 100,000 francs to anyone who was the first to communicate with a celestial body, with the exception of Mars, which would be too easy. During the Roaring Twenties, scattered radio signals thought to come from Mars inspired a touch of Mars mania in the Chief of Naval Operations, Admiral Eberle. He ordered many of the navy's huge radio stations to shut down transmissions for three days in August 1924 and listen for signals from Martians. Standing by to translate was the chief of the code section for the Army Signal Corps, who didn't crack any codes then but went on, Sinnott tells us, to crack the Japanese diplomatic code *Purple* just before World War II.

Two years later, in 1926, a Dr. Robinson in Hertfordshire, England, said he'd finally been in communication with Mars' inhabitants. During an interview, Robinson claimed that Martians had big ears, long hair, and Chinese features and that they smoked pipes, drank tea, and drove cars with weatherproof hoods. According to Sinnott, reporters walked out when Robinson started describing Martian "lower life forms." The notion of intelligent life on Mars had cooled down considerably by the 1930s, but not the notion of life itself.

The first successful flyby of the planet Mars was made in 1965 by the *Mariner 4* spacecraft. It was the first to transmit close-up pictures of the planet's surface. *Mariner 9* continued the effort in 1971, and the Martian features thus documented were given non-Anglo names, such as Mangala, Mawrlth, Simud, and Maja (from Sanskrit, Welsh, Sumerian, and Nepali, respectively). Until September, with the launch of the Mars *Observer* spacecraft, the last missions to Mars had been the two *Viking* landings made in 1976. The *Viking* landers analyzed the surface of the planet. With all their own "miraculous feats of engineering" and technology, they were unable to prove conclusively whether life on Mars exists.

The Mars *Observer* spacecraft is scheduled to begin studying the planet when it arrives late in 1993. It will be placed in a low polar orbit and will study the planet's atmosphere, surface, and interior over the course of one complete Martian year—equivalent to two Earth-years. In late 1995, with the planned arrival of two Russian spacecraft carrying deployable balloons and surface packages, the Mars *Observer* will begin to relay data back to Earth from these experiments. This information will sharpen our understanding of the similarities and differences among Earth, Mars, and Venus and will help lay the foundations for future expeditions to the red planet. Given the curious history of our interest in this planet, it is somewhat ironic, astronomers point out, that if we ever get there in a manned mission, we will be the Martians.

THE PLANETS IN JANUARY

Mercury rises less than an hour before sunrise at the beginning of the month and is very low in the southeast just before dawn. By midmonth, the planet is too close to the sun to be seen, reaching superior conjunction (slipping behind the sun from the earth's point of view) on the 23d.

science teacher, emphasizes the program's usefulness in education, describing among other things how to print unlabeled constellation charts to help students learn their way around the night sky. But the principal use of *Deep Space* is as a deep-space aid for the involved amateur. As a DOS program, it does without the friendly graphic design familiar to users of Windows or Macintosh operating systems; this austerity can make it a bit difficult to use at first. Nevertheless, *Deep Space* has emerged as a favorite among those who want a program that incorporates a big database and can interface with their mammoth telescopes.

MegaStar is quite limited in some ways. It cannot show a piece of sky larger than 20 degrees. It has never heard of the moon and is ignorant of every planet save Pluto. It offers nothing in the way of pretty pictures or video animations. But within these limitations it emerges as an impressive tool for the earnest student of the sky. It can link up to a computer-controlled telescope, and its functions are well organized for easy use by a bleary-eyed observer who has been awake most of the night. Its data filters make it simple to generate displays tailored to the observer's interests and to prevailing conditions—for example, one can eliminate all stars dimmer than the limits of one's equipment. An "eyepiece" function conveniently replicates the view through the telescope. *MegaStar* can be employed to print out star charts that simply blow away anything commercially available in hard-copy form. For a study of the rich Virgo cluster of galaxies, I printed and pasted together nine adjacent *MegaStar* charts. The result was a document any extragalactic observer would envy and one few could have readily obtained before.

All these programs have their glitches. Some—*Distant Suns,* for instance—look a lot better on-screen than they do on a printout. Each excels at specific tasks where others falter. Buffs on a budget would do well to consult with the local astronomy club and see the software packages in action before making a purchase. But stargazers who find one that fills their needs will soon wonder how they ever got along without it. These disks show what CD-ROM technology can do when used not as a flashy attempt to imitate Hollywood movies but as a down-to-earth means for bringing professional-caliber scientific tools to the general public.

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Rethinking Green Thoughts

Review by Thomas E. Lovejoy

A MOMENT ON THE EARTH: THE COMING AGE OF ENVIRONMENTAL OPTIMISM, by Gregg Easterbrook. Viking Penguin, 1995 ($27.95). **NOAH'S CHOICE: THE FUTURE OF ENDANGERED SPECIES,** by Charles C. Mann and Mark L. Plummer. Alfred A. Knopf, 1995 ($24). **LOSING GROUND: AMERICAN ENVIRONMENTALISM AT THE CLOSE OF THE TWENTIETH CENTURY,** by Mark Dowie. MIT Press, 1995 ($25).

The modern environmental movement has achieved some remarkable successes. These days we almost take it for granted that automobiles should be as clean as possible, that some pesticides are too dangerous to use, that governments should act to protect the ozone layer. Now it seems that the moment has arrived when an evaluation of the strengths and weaknesses of the environmental agenda is due, perhaps even overdue. These three volumes are prominent among a considerable, recent spate of such reevaluations. Gregg Easterbrook examines environmentalism generally; Charles C. Mann and Mark L. Plummer focus on biological diversity in the U.S., most particularly on the Endangered Species Act; Mark Dowie looks at the history and political science of the American environmental movement. Taken together these books paint a fascinating portrait of the perceptions and realities of environmentalism, especially in the U.S., and of the challenges now facing the movement.

Many of my colleagues have been upset by *A Moment on the Earth.* In the book, Easterbrook advances what he calls the "Ecorealist Manifesto," a program of reduced governmental intervention based on the notion that many current environmental crises are not so dire as commonly claimed. I anticipated that I would disagree with some of Easterbrook's ideas, but I also expected to find important ones. In general, however, I was stunningly disappointed by the book's rambling prose and profusion of inconsistency and error.

Near the beginning of the book, for example, Easterbrook faults Rachel Carson for predicting that American robins would be seriously reduced by pesticides and claims that "nothing Carson forecast in *Silent Spring* came to pass." Yes, much of what Carson forecast did not come to pass. Why? Because she raised the alarm about the risks of chlorinated hydrocarbons early on, before scientists understood the mechanism by which those substances strangle the calcium metabolism of birds at the ends of long food chains (such as various birds of prey and the brown pelican). That warning inspired research that advanced knowledge of pesticide risks from correlation to causality.

Refined understanding in turn led to policy changes—most notably the banning of chlorinated hydrocarbons such as DDT—that enabled the affected species to recover. Easterbrook himself reports that the bald eagle population is now growing at 5.4 percent annually, while ignoring its previous downward trend, which was reversed only after the harmful pesticides were made illegal. He also extolls the recovery of the peregrine falcon and its reintroduction to New York City. Surely these qualify as environmental science and policy success stories.

It is hard to comprehend how a reporter like Easterbrook, who has followed environmental matters for years, could have failed to grasp such a fundamental issue as this one. He (as well as Mann and Plummer in *Noah's Choice*) misunderstands the essential purpose of bleak projections such as those publicized by Carson—namely, to highlight unfavorable trends so that the potential calamities will not come to pass. Sad to say, it is in fact quite rare for such projections to be totally wrong. To dismiss such efforts as doomsaying, and to portray the brave and prescient individuals who raise such warnings as biological Cassandras, does a disservice to society.

Easterbrook does make some significant points in *A Moment on the Earth.* He is correct that environmentalists have scored some major triumphs, such as achieving measurably cleaner air and water in the U.S. and in some other parts of the world. This country possesses an impressive set of environmental laws, although many of these are coming under fire. Far-reaching international agreements watch over the ozone layer, climate change and biodiversity. The numerous environmental successes give us just cause to be proud, but they do tend to get taken for granted. News, at least what people most vividly remember, is more about problems and moments of peril than about increments of progress. We all need some retrospection, caught up as we are in the daily hurly-burly, if we are to appreciate the overall improvements; Easterbrook's recounting of how far we have come serves a useful function.

Easterbrook touches on another noteworthy topic when he chastises environmentalists for overlooking problems of developing nations: drinkable water, clean air, food supply, disease control. Some of his criticisms are on target, although a lot of the sustainable development guidelines that emerged from the United Nations Earth Summit in Rio de Janeiro do speak to these points, and multilateral development plans have increasingly taken them into consideration. He is wrong, however, to question the prominence of climate change as an environmental issue at Rio: this problem is one that can be addressed only at the international level.

Again and again, Easterbrook fails to grapple with the complexity of the topics he raises. He is rightly optimistic about clean technology, but his belief that "almost every pollution issue will be solved within the lifetimes of readers of this book" seems overly exuberant. The Delaney clause, a seemingly sensible guideline that prohibits carcinogens in food at any level of detectability, approaches never-never land because of ever improving detection technology; there is no simple solution to setting a "safe" level of carcinogens.

The Ecorealist Manifesto gives high priority to conserving biodiversity because of the irreversibility of extinction—in itself, an admirable stance. Yet Easterbrook's book seems not to recognize a primary implication of his goal, that harder problems relating to the use of land and waters lie ahead.

The overall problem with *A Moment on the Earth* is that it consists of such a jumble of value judgments, anecdotes and errors that the constructive thoughts are often obscured. Easterbrook's most absurd assertion, building from a misunderstanding of evolutionary biologist Lynn Margulis's work, is that cooperation is dominant in nature. That notion completely ignores the existence of food chains, competition and disease. Yes, there are a lot of social insects, but vaguely mentioning that "for instance, deer greatly outnumber wolves" does not prove that "cooperative species are far more numerous than combative species and usually have larger populations." There are also problems of sheer sloppiness. It is hard to believe an editor overlooked the nonsense geography of the statement that "the North American population when Columbus landed may have been as high as 100 million, with most of this number living in Central and South America."

The innumerable errors and careless assertions are all the more frustrating because *A Moment on the Earth* could have been so much better. Easterbrook is obviously well versed in environmental matters, and he could have packed an enormous amount of information into the book's 698-page text. Yet he leaves potentially important topics undeveloped, such as the question of why environmentalists worry about the development of immunity in species targeted by pesticides but do not count on such immunity developing in nontarget species.

This book is so long and muddled that I suspect few people will plow through it in its entirety—and therein lies its danger. A casual reading could lead to the conclusion that all environmental problems have been solved. The novitiate and casual layperson who recognizes some of Easterbrook's numerous mistakes will find it hard to sort out the valid from the invalid. And it is unfortunate that the book excludes most names of people from the index.

SHAHN KERMANI *Gamma Liaison*

PROTESTERS DENOUNCE logging in old-growth forests in Oregon. Such controversies have promoted an unfortunate caricature of environmentalists as antibusiness extremists.

In contrast with the broad but addled *A Moment on the Earth, Noah's Choice* is superbly written but disingenuously selective. The book deals, as its title implies, with biodiversity conservation in the context of the Endangered Species Act. The act is best known to the public from a handful of highly publicized instances (such as the efforts to protect the snail darter from the effects of the Tellico Dam) in which a vested interest came head-to-head with an endangered plant or animal having an esoteric, easily ridiculed name. From such stories, one might readily conclude that protecting endangered species comes down to a question of the future of the spotted owl versus jobs for loggers. For those unfamiliar with the true situation, the act seems severely tilted against people.

This kind of choice—protecting the ecosystem or safeguarding human interests—is the focus of Mann and Plummer's outstandingly readable book. *Noah's Choice* opens with an account of the discovery of the rare American burying beetle (which has a fascinating natural history) in Oklahoma and the difficulties that ensue as regulations dictated by the Endangered Species Act threaten to terminate the construction of a new highway. The authors follow with a couple of chapters that provide background information on biological diversity, the classification of organisms and estimation of extinctions.

Mann and Plummer, like Easterbrook, find it confusing to reconcile the relatively small number of officially acknowledged extinctions with projections—one of which I made in 1980—that major extinctions loom in the near future. Their book presents a lucid and reasonably fair discussion of species-versus-area curves, a common method for estimating biodiversity and projecting extinctions. Mann and Plummer reflect the debate over those estimates much better than Easterbrook does. But all three authors seem not to understand that the organizations that "officially" confer extinction status are enormously conservative; they often wait for decades before pronouncing a species extinct. Also, many biodiversity projections take into account the numerous extinctions that will occur once the remnant populations living in isolated fragments eventually wink out. Such losses are inevitable unless something is done to alter the situation.

Mann and Plummer's examples of endangered species and ecosystems—the American burying beetle, the Karner Blue butterfly, the Balcones Canyonlands development in Texas—are all difficult ones in which it is easy to empathize with local people caught up in the exercise. Although these instances are undeniable and represent one kind of experience, it seems unfair that the authors give little representation to the multitude of success stories, said to number in the tens of thousands, in which matters worked out reasonably.

The Endangered Species Act is portrayed as unsuccessful because the number of species being added to the list is so much larger than the number removed. That imbalance is more a matter of the act trying to catch up with reality than anything else. *Noah's Choice* also contains whiffs of the old humans-versus-environment illusion, and the use of modifiers seems unnecessarily value-laden: "slimy things," "creepy crawlies," "shrieking predictions."

Mann and Plummer offer various suggestions about how to proceed in the future, but for the most part they seem to ignore the difference between flaws in the Endangered Species Act per se and problems with how it has been used. In 1978 Wildlife and America prophetically noted that when the act is "used to combat all that is wrong about society's approach to the environment, the legislation stands in danger of losing public support and being weakened."

In reality, the biggest obstacle to saving endangered species has been the lack of intervention until a conservation situation grows so serious that it demands invoking the regulatory powers of the act. During the 1980s, for example, the conservation community warned about the status and unfavorable trends of old-growth forests in the Northwest, but the federal government did nothing. Instead the situation languished and deteriorated until the spotted owl qualified as the first endangered species of the ecosystem. The government could have designed a much better compromise of economic and conservation interests if it had acted earlier. The Northwest forest plan came just in the nick of time for a large number of species. The biodiversity of those forests now will survive only with a great deal of on-the-ground survey work and ongoing management.

Like Easterbrook, Mann and Plummer recognize the value of biodiversity conservation. They endorse the visionary effort, spearheaded by Secretary of the Interior Bruce Babbitt, to create a National Biological Survey. They also recognize that "Noah's Principle" (to save every species) is unattainable. Consequently, they offer "Noah's Choice," a way to make fundamentally impossible biological choices in a politically feasible manner. Their plan emphasizes prohibiting harm to individuals of endangered species over limiting the destruction of those species' habitat. The authors overlook the slippery slope this approach would invite: their scheme would automatically expand the list of endangered species (the individuals of which cannot be harmed) while offering no protection to the ecosystem in which those species live. The result, in all likelihood, would be a ballooning list of endangered species and an enforcement and management nightmare.

The "Noah's Choice" solution encourages procrastination, waiting until there is a problem rather than trying to avoid creating one in the first place. As a possible offset, the authors suggest protecting biodiversity on public land. That plan works fine for Nevada, 83 percent of which is federal land, but hardly at all for Texas, which has almost none. More promising is Mann and Plummer's proposal for the formation of a national biodiversity trust, which could provide incentives for private landowners. Part of the difficulty so far has certainly been that current laws impose costs on a few to generate benefits for many. Efforts to conserve biodiversity tend to come into conflict with our system of private property and especially with the plight of the small landowner. It is one of the most fundamental conundrums of environmental regulation.

The unflinching historical view in *Losing Ground* may have ruffled its own share of environmental feathers, but the book is well written, thought-provoking and plows the most new ground of the three. Mark Dowie, a former editor at *Mother Jones,* divides the history of environmentalism in the U.S. into four periods, which he terms waves. The first consisted of private individuals who were engaged in conservation (but certainly Theodore Roosevelt took it firmly into the public realm). In the second, it became an environmental political movement, starting in the mid-1960s and ending when it hit the wall of the Reagan administration.

Dowie focuses most of his attention on the third wave, from the 1980s to the present; he is harshly critical of much of what he sees. As it gained professional status, the environmental movement lost passion. Fund-raising gained ascendancy over ecological vision. The movement got too close to the corporate world and succumbed too easily to compromise. It remained an elitist group, paying little attention to poor neighborhoods, ethnic groups, environmental justice or the stark poverty of Third World nations. There is sufficient truth to all of the above to strike home, but environmentalism has never been monochromatic. Significant exceptions also exist to most of the above. That said, these attacks represent real challenges that must be dealt with in a clear-eyed manner, for they restrict the movement's effectiveness.

There are plenty of irritating errors in *Losing Ground,* but they are mostly ones of interpretation rather than of scientific fact. The collaboration between Conoco and the Natural Resources Defense Council in Ecuador is much more about learning to work with indigenous peoples than about giving in to industry or self-importance, as Dowie asserts. Market incentives and emissions trading, described in a section called "A Market for 'Bads,'" are yielding successes as well as valuable experiences about how to fine-tune such approaches. A discussion of Vice President Al Gore's potentially misleading remark linking environment and health issues does not accurately reflect his evident, deep understanding of the linkage. The description of the Northwest forest plan is relatively one-sided, giving a false impression that many environmentalists and the Clinton administration caved in to logging interests.

Dowie ends the book with his view of an emerging fourth wave. Its main characteristic is a swing, already under way, back toward the grass roots. Dowie broadly anticipates what the new environmentalism will encompass, including some very pragmatic elements and some fundamental value shifts. My main criticism of his vision is that it will not work by itself: it will need the assistance of the third-wave types who work on national policy and government standards; no effort will succeed without the committed involvement of the private sector as well.

All three of these books will make a lot of environmentalists unhappy. *Noah's Choice* and especially *A Moment on the Earth* display a surprising lack of understanding about how science works: perpetually self-testing, advancing by hypothesis and critical examination, inconveniently nonlinear but wonderfully up front about uncertainty. By and large, humanity acts as if the scientific method is disconnected from our daily lives, and yet a wider awareness of that method would help greatly in framing the current environmental debates.

I hope many environmental professionals will read these books and winnow out some crucial messages we should be thinking about. These kinds of reevaluations have mostly appeared in the U.S., perhaps reflecting the progress of American environmentalism or our own particular national style. In any case, these books show that we have not been listening enough. We have become portrayed as extremists saying, "Don't. Stop. You can't do this," when our real motivation is conservation of opportunity for health, wealth and a better future. We must get that message across if the movement is to persevere.

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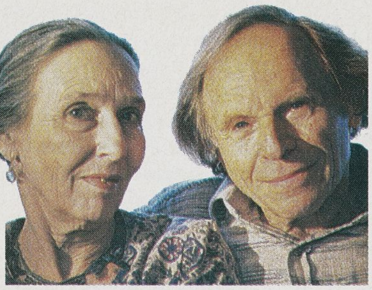

WONDERS

by Phylis and Philip Morrison

The Physics of Binary Numbers

The label we give the millennial turn of the calendar looming ahead is a string of four digits, written as 2000 in the everyday convention of number base 10 (of course, the true new millennium begins a year later on January 1, 2001—fine for purists, but a less aesthetically pleasing number). Count leftward from the right-hand end: at the zero power of 10, enter no 1's (that is, place a 0 there); none either at the first power of 10; the second power, again none. But for the third power—10^3, or 1,000—you want to count two of them. Total: two times 10^3 and no more, thus 2,000. You need to distinguish just 10 digits in this scheme: 0, 1, 2, 3, 4, 5, 6, 7, 8, 9. String them out as far as you like; each place has meaning.

There are simpler number bases that one could choose. Try the choice closest to primordial, just a set of identical strokes, ||||||||||||||||||||... and so on, using only one form of mark, base 1. Now you need a string of 2,000 strokes, dozens of lines of type, nearly uncountable and unusable. Would you prefer a recipe *alla romana?* That is easy: 2,000 becomes just MM. The ancient Romans also used repeated strings, as in MDCCCCLXXXXVI, supplemented with a few more symbols. The mix is quite practical. What they did recalls the assembly of chemical elements that make up the natural world: interminable arrays of atoms spell out all the varieties of matter as repetitive piles composed of fewer than 100 different symbols, rather in the Roman way but without arithmetic.

Try a modern practicality, hexadecimal numbers, base 16. (Consult the calculator held in your computer software; you will find hexadecimal math lurking there.) The number we call 2,000, when written out in conventional hex, is $7D0 = 7(16^2) + 13(16^1) + 0(16^0)$, where the 10 decimal digits are supplemented by six letters, A through F, to make a total of 16 alphanumeric symbols.

Finally, we have the binary numbers, base 2, needing only two digits, 1 and 0 (or on-off, true-false and many another dichotomy). To write the year name in binary, pure machine discourse, first note that it factors into 250×8 and that multiplication is very easy in base 2. Thus, $250 = 128 + 64 + 32 + 16 + 8 + 2$, which is $2^7 + 2^6 + 2^5 + 2^4 + 2^3 + 0(2^2) + 2^1 + 0(2^0)$, or 11111010 in base 2 notation. Multiply that by 1000 (the way you would write eight, 2^3, in base 2), to find 11111010000 for 2,000—a simple enough process, if longish.

The choice of base is plainly open to meet our needs. The tally of line strokes—an unwieldy string all of one single symbol—uses the minimal list of digits, just one. It has the longest strings but of the simplest sort. At the other extreme lies a maximal scheme whose list of distinct "digits" is unending: every number becomes its own one-place symbol. Placeholding vanishes; all numbers have only one digit, the shortest possible, but there is an interminable symbol list to learn.

Matter, gravity and the simplest symmetry of life lead directly to the binary numbers.

The fertile metaphysical imagination of the Argentine writer Jorge Luis Borges conjured up a character whose mind was able to fathom that logical limit. In his short story "Funes, the Memorious," Borges introduces us to a poor young Uruguayan, a hapless, friendless prodigy by the name of Ireneo Funes. His blessing and curse was that he could forget nothing. Where we might "perceive at a glance three wineglasses on the table, Funes saw all the shoots, clusters, and grapes of the vine." He could easily envision in memory every visible star in the sky. His arithmetic had no placeholders, only arbitrary names corresponding to every number. To count to 7,013, he said, "*Máximo Perez,*" and for 7,014, he said, "*The Train.*" Funes the Memorious employed an unending number base—every number a new symbol, unrelated to any other, without computational structure. Ordinary people cannot learn an unending list of such complicated symbols; Funes's system was just as pure and just as impractical as the opposite limit, base 1.

The minimal useful number base, base 2, forms the underpinning of binary logic and digital computing. Logic is a splendid path to mathematics, but in fact the oldest known use of binary notation was derived not from logic nor from abstraction but arose, surprisingly, from a strictly physical use in the Indus River cities of the Harappān culture, more than four millennia back.

Between the world wars, the Boston Museum of Fine Arts dug in the big, brick-built ruins of Mohenjo-Daro, once a great city, on the Indus. Among the other finds, an odd assortment that the museum displayed in a small glass case caught our attention years ago. At first glance, it seemed only half a dozen pebbles, such as any child might collect. Not quite: it was a display of weights used in the beadmakers' quarter of that old city, long a center for the export of beads, often the mineral carnelian, an ancient specialty of the region.

The case contained a nice set of carefully made stone cubes and a few other examples of formal weights. But what was that handful of unworked pebbles? Although they were in no way modified by the hand of their ancient collectors, these stones were nonetheless a set of weights, having closely correct weight ratios that doubled along the set in the pattern, 1, 1, 2, 4, 8, 16.... The ancient weights were much like those still in use today; in fact, the Harappan's fundamental unit was just a little lighter than our modern ounce. Here is an artifact of pure information from the mind of the long-vanished collector. It seems likely that our old European standard of 16 ounces to the pound is a relic of the same idea. We cannot say whether it was shared across the millennia or reinvented by independent craftsmen, located far apart, solving a parallel problem of measurement.

Phylis visited the glacier-borne pebbles that litter the South Beach of Martha's Vineyard, part of the great terminal moraine left behind by the retreating ice sheets from the last Ice Age. There she undertook to replicate those artifacts so cleverly assembled by the Indus people long ago. She first made the instrument we know lies behind the pebble weights: the equal-arm balance, examples of which are found among the Indus ruins and which remain in

Perspectives

Conservation: Tactics for a Constant Crisis

MICHAEL E. SOULÉ

IS WILDLIFE CONSERVATION FAILING? IN THE UNITED STATES, species diversity appears to be declining at an accelerating rate (*1*). Even the Endangered Species Act of 1973 (ESA) has not significantly slowed the deterioration of the nation's biological estate, although this is largely the result of lack of support from the federal administration. Currently there are over 4000 species and subspecies recognized as candidates for endangered species status, but the listing process administered by the U.S. Fish and Wildlife Service is bogged down because of lack of funding. There are no recovery plans for nearly half of the 600 or so species in the United States that have been officially listed as threatened or endangered, and the score or so of recovering species is balanced by an equal number that may be extinct (*2*).

The situation is generally much worse in other nations. Biologists with extensive experience in developing countries are saying that by almost any quantitative standard conservation is failing, and that current approaches to conservation, such as traditional parks and reserves, are unlikely to succeed (*3, 4*). Worldwide, only about 3% of the land is set aside in 5000 nature reserves or protected areas (*5*), but many of these reserves are deteriorating (*6*). Because the moist tropics are far richer in species diversity than other biogeographic regions, and because deforestation will probably eliminate almost all of the tropical forests outside of protected areas by 2100 (7), biogeographers estimate that from 25 to 50% or more of tropical species will vanish in the next century or sooner (Fig. 1) (*8*). Even if humanity were to depart the earth, recovery of biotic diversity by evolutionary mechanisms would require millions of years, depending on how deep, taxonomically, the extinction crisis cuts (*9*).

Such dire predictions are now leading to a reappraisal of conservation's goals and tactics. In this article, I conclude that this reappraisal would be more fruitful if there were a deeper appreciation of the biological and social contexts of conservation actions, particularly how both biogeography and political geography dictate different conservation tactics in different situations. I also argue for an actuarial approach to the viability of protected areas—one that considers the social factors determining the half-life of nature reserves.

The Biospatial Hierarchy

Effective conservation is impossible without some knowledge of biotic (biological) diversity (biodiversity). For most scientific purposes, "life" is classified taxonomically, based on similarity and presumed evolutionary relationship. For purposes of protection, however, the living components of nature are usually classified in a "biospatial" hierarchy of nested sets. In practice, there are about five levels to this hierarchy: (i) whole systems at the landscape or ecosystems levels, (ii) assemblages (associations and communities), (iii) species, (iv) populations, and (v) genes (*10*). Place, not evolutionary relationship, is the basis for the biospatial hierarchy, because most conservation strategies are geographically anchored (*11, 12*).

The targets at the top of the biospatial hierarchy are ecosystems (or landscapes and seascapes making up interacting ecosystems), including such topographic features as entire drainages. A frequently cited example is the Yellowstone National Park region, including the adjacent Grand Teton National Park and other federally managed lands. Ideally, ecosystem conservation protects the contained biotic communities: habitats, species, populations, and genes, not to mention all ecological interactions, processes, and some of the traditional, human cultural practices that have been historically associated with the ecosystem.

At the second level, an arbitrary number of biotic assemblages can be defined within ecosystems, although the species themselves show little correlation in their distributions when climate changes (*13*). Nevertheless, state, federal, and international conservation programs often base their conservation strategies on the completion of the network of biotic community types—the so-called coarse-filter approach. The discovery of "gaps" in the network of assemblages is most often based on systems of biogeographic classification (*12, 14*).

The third biospatial level, species, is defined as groups of populations that routinely exchange genes or are phenotypically similar (*15*). The selection of protected areas is frequently based on the presence of one or more endangered species, often large-bodied or attractive ones. In addition, regions with high species diversity, such as tropical forests, coral reefs, or regions with large proportions of local endemic species, such as isolated mountain ranges or oceanic islands, are frequently identified as targets of conservation. Another reason for focusing on species is that the management of protected areas is often facilitated by attending to a relatively small number of so-called keystone or indicator species; these species may not be endangered themselves, but they are used to monitor the status of a much larger assemblage of species (*16–18*).

Next is populations. Populations, whether mobile or sedentary, are dynamic assemblages of individuals which maintain genetic and sometimes social information in lineages that may ramify and merge as individuals are born, reproduce, and die. Endangered populations, and those of species that mediate important ecological processes, are often targets of conservation, so that their viability is a major concern (*18, 19*). Theoretical treatments of population viability are influencing public policy, such as the debate over the spotted owl in the Pacific Northwest (*20*).

At the small end of the biospatial hierarchy of conservation targets are genes. Genes are sometimes conserved ex situ (*21, 22*) as seed collections, in tissue culture or germplasm collections, or as cryopreserved semen, ova, embryos, and tissues. The extraction of genes from nature annually produces multibillion dollar benefits for agriculture, biotechnology, and public health (*23*). In nature, genetic

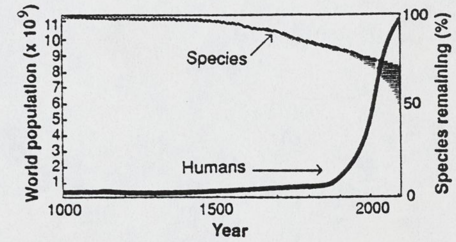

Fig. 1. The expected inverse correlation between human population size and the survival of species worldwide. Extinction rates depend on the size of the habitat fragment and occur at a decreasing rate as habitat fragments age. Anthropogenic extinctions before A.D. 1000 are ignored. The shape and width of the extinction curve reflect the uncertainty of the predictions; the curve is based in part on the assumption that most of the extinct species will be small organisms with geographically limited distributions.

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variation maintains the fitness and evolutionary flexibility of natural populations (*16*). Reserves in seminatural areas have been set aside to preserve the wild relatives of commercially important plants, especially to protect genes and gene combinations providing resistance to pests, drought, and other climatic factors (*24*).

The Six Classes of Interference and the North-South Distinction

The five levels of the biospatial hierarchy—are being undermined by six major classes of human interference (*25*), as shown in Fig. 2. These six factors are (i) the loss of habitat; (ii) the fragmentation of habitat-producing deleterious area, edge, demographic, and genetic effects; (iii) overexploitation; (iv) the spread of exotic (introduced and alien) species and diseases; (v) air, soil, and water pollution; and (vi) climate change. These factors have all been discussed in great detail (*16, 19, 22, 26, 27*). The intensities of shading in the two parts of Fig. 2 are subjective, but suggest that the present and future hazards posed by the six factors are not equal in strength or concordant in rank across the range of conservation targets, or from economically poorer to economically richer nations.

Clearly the impact of a given factor depends on the time, the place, and the circumstances. As indicated in Fig. 2, economics, culture, as well as the temperate-tropical disparity in species diversity and other biogeographic patterns, explain the differences in biotic vulnerability between tropical, poor countries, and temperate, wealthier ones. The vastly greater number of species in the tropical nations, the much smaller geographic ranges of tropical species on average (*28*), in addition to the high rates of habitat destruction in most of these countries, means that species in the tropics are particularly vulnerable to habitat loss and fragmentation. Similarly, not all parts of the planet will be equally susceptible to the impacts of acid rain, ozone thinning, or greenhouse warming; for example, the effects of greenhouse warming will be much greater at high than low latitudes, except, perhaps, for marine systems (*29*). Other aspects of biogeography are relevant to geographic heterogeneity in biotic vulnerability; on oceanic islands, for example, introduced predators are typically more damaging than on continents (*16, 25, 30*), and introduced animals (goats, pigs, rats, mongooses, snakes, and predatory snails for instance) and plants may have catastrophic effects (*31*).

Although it is difficult to generalize, one can point to some rough principles about the global vulnerability of terrestrial biodiversity (*32*). Habitat loss, fragmentation, and the direct and indirect effects of exotic species are problems everywhere (Fig. 2A), but overharvesting of economically important species is now of greater concern in poorer countries. Pollution and climate pose major threats in the temperate zone nations (Fig. 2B). As discussed below, north-south differences in socioeconomic variables and biogeography mean that conservation tactics must be tailored to the location.

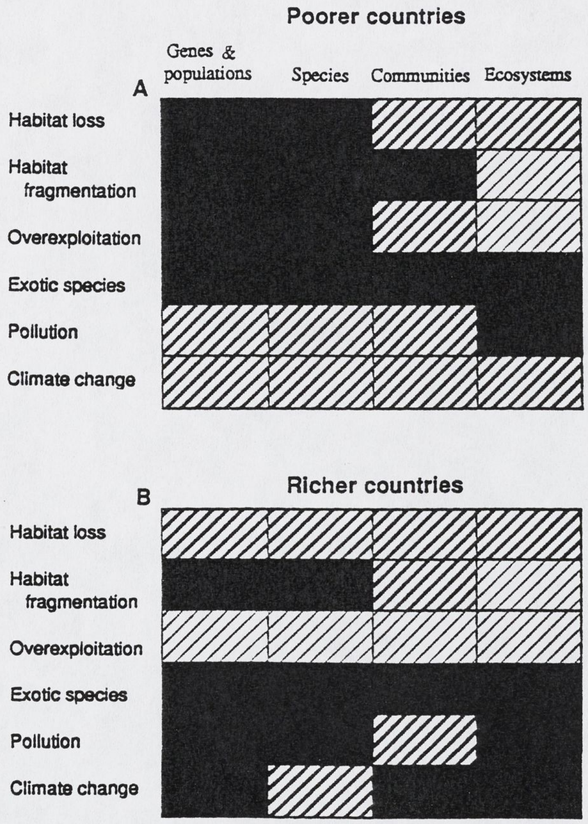

Fig. 2. Relative impacts of factors affecting terrestrial biotic diversity in (**A**) poor and (**B**) rich countries. Shading indicates intensity of impact: solid = highest; thick lines = intermediate; thin lines = lowest. Ecosystems refers to landscape level formations including, for example, mangrove habitats, coral reefs, riverine/riparian systems, forests, and savannas. The distribution of impacts on aquatic and marine systems differs somewhat from those shown here.

The Seven Sources of Biotic Degradation

The six classes of interference may constitute the most obvious proximal causes of biotic attrition, but the more fundamental causes are rooted in the contemporary human condition, especially as they are amplified by the explosive growth in human numbers in the last three centuries (Fig. 1). These more fundamental causes are listed in Table 1. The following brief descriptions of these factors are neither systematic nor exhaustive, but even this superficial treatment demonstrates why simple approaches (such as a network of protected areas alone) will fail.

Population growth. The continuous increase in human numbers exacerbates nearly every other environmental problem (*33, 34*). The population reached 1 billion about 1800, and appears to be headed toward 10 billion by 2046 and 12 billion by 2100, according to recent World Bank and United Nations projections. Ecologists argue that such numbers are incompatible with many ecological and evolutionary processes, including the persistence of large predators, the continuation of annual migrations of birds (*35*), speciation in large organisms (*36*), and the protection and maintenance of native biotas in the face of increasing pressure from human beings and

Table 1. Categories of fundamental human factors that contribute to the erosion of biological diversity.

Factor	Example of impact on conservation
Population growth	Population pressures
Poverty	Hunger, deforestation, trade in rare and endangered species, failure of grass roots support
Misperception	Desire for quick results and denial of long-term failures
Anthropocentrism	Lack of support for nonutilitarian causes
Cultural transitions	Unsustainable resource management during colonization and rapid social change
Economics	Failure of planning because of internationalization of markets and erratic pricing of commodities
Policy implementation	Civil disruption, wars, corruption, failure of law enforcement

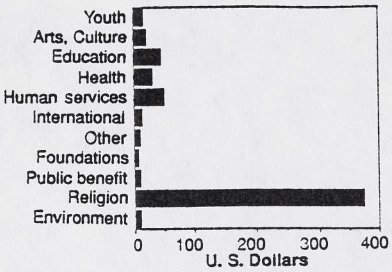

Fig. 3. Average charitable contributions per household in the United States. [Adapted from (*67*)]

introduced species. For nonhuman species, this "demographic winter" will last until human beings decide to reduce their numbers to levels compatible with the restoration of pre-explosion biotic processes (*37*). Human populations are already declining in many industrialized countries.

Poverty. The problem is not merely the shear magnitude of human numbers, however; it is compounded by poverty, the aspirations of people the world over for a better quality of life, and by social and political forces that impede the smooth transition to minimum (let alone "optimal") levels of prosperity, health, and justice (*38*). Disparities in income produce disparities of impacts. The per capita contribution to atmospheric pollution (and, hence, global climate change) is often orders of magnitude higher for citizens of the industrialized countries than for those in poorer nations (*34*), and economic pressures from the former contribute to unsustainable land use practices in the latter. Habitat destruction and extinction, however, will occur most rapidly in the tropics (Fig. 2A), where lack of economic opportunity, demographic momentum, and restrictions on reproductive choice are the engines that power the destruction of life.

It is probable that the price of raising human economic welfare to a standard similar to that in the wealthier countries will be biotic devastation in the tropics on a scale inconsistent with the persistence of wildlands except, perhaps, in remote, nonarable regions (*39*). Ehrlich and Wilson (*40*) point out that the magnitude of human aspirations, including demands on natural resources, if multiplied by the expected increases in human numbers, would require the human co-option of most remaining wildlands for grazing, farming, energy production, mining, transportation, and other uses. Therefore, the loss of most tropical wildlands in the next 50 years or so, an epochal catastrophe for earthly life, appears a virtual inevitability.

Misperception and time scale. Gradual environmental degradation goes almost unnoticed (*41*), whereas governments often overreact to sudden events of lesser overall impact. This short-term mentality is also reflected in current social mores and public policies favoring quick profits and results. The problem is that the benefits of conservation projects can only be measured on a scale of centuries. This difference in time scales between economic development projects and some conservation projects leads to conflicts because the business of conservation is keeping options open, whereas business as usual (economic development) often forecloses them.

Anthropocentrism. Many conservationists argue that current cultural values are antithetical to effective conservation policies, and that a new ethic or a revolutionary change in human consciousness is necessary before significant progress is possible (*42*). There are many calls for less human-centered, more biocentric economic policies. The anthropocentric orientation of most societies (*43*) however, augurs poorly for behavioral revolutions. If charitable donations reflect how Americans rank society's needs, it is evident that humanitarian concerns are dominant; money flows primarily to religious organizations and to medical, cultural, and social welfare causes. Figure 3 shows that only 1.5% of donated monies go to support environmental (nonhuman) groups and causes. This percentage is likely to increase, though, as donors learn about the environmental foundations of physical and social welfare.

Mindful of biases favoring our own species, nearly every book, report, or "strategy" written to promote or guide the conservation of biodiversity presents a list of utilitarian justifications, including the free services and amenities provided by nature (for example, water purification and storage, habitat for fish and livestock, vistas), and the promise of life-extending pharmaceuticals and agro-industrial products that are yet undiscovered in the tissues of organisms (*23*). Unfortunately, the political effectiveness of narrowly utilitarian arguments for large protected areas in the tropics and elsewhere is weak, in part because the promise of long-term economic and health benefits to society as a whole appears abstract to individuals and corporations more concerned with survival and short-term economic gains.

Cultural transitions. The most destructive cultures, environmentally, appear to be those that are colonizing uninhabited territory and those that are in a stage of rapid cultural (often technological) transition (*44*). The cultural groups that appear to be the least destructive to natural systems are those that have been occupying the same place for centuries or more (*45*). Overharvesting of wild animals, of aquatic and marine organisms, and of forests, is predictable, therefore, when human groups (i) have little or no experience in their current geographic setting or (ii) are undergoing integration into the world economy. Wealthy, well-educated, industrialized cultures may have the potential for minimizing environmental damage, but show little promise of this at present. Because most of the world's people are not only poor, but in a transitional phase between traditional agrarian self-sufficiency and a modern, high-input agricultural or industrial-urban society, relatively little value is placed on the protection of nature, and even where nature is highly valued, such valuation is often left out of economic calculus.

Economics. Environmental destruction and the erosion of biological diversity in the tropics and elsewhere is exacerbated by systems of commerce that create demands from the industrialized north for products, the production of which causes massive habitat destruction (*46*). The "cool chain" industry, for example, produces fresh produce such as fruit, vegetables, cut flowers, and mariculture produce (such as, shrimp) in the poorer countries and ships them in refrigerated carriers to the richer countries (*47*). This new industry contributes to the destruction of many habitats including lowland forests, mangrove, estuarine, and reef habitats. Better known are the coffee, sugar cane, banana, cacao, forest products, and cattle industries that account for the loss of a large proportion of tropical forests in developing countries (*23, 48*). In addition, a major contributor to forest and woodland destruction is the cutting of trees for the production of fuel wood and charcoal for domestic cooking and heating uses. Before the international price-fixing agreements among petroleum producers, most people in developing countries could afford to cook with kerosene. Now they must rely on wood, charcoal, and dung, contributing to the deterioration of forests and soils (*49*).

Notwithstanding the grave moral, social, and geopolitical implications of current economic disparities, the redress of such imbalances is unlikely to occur in time to save most seminatural biological systems from massive attrition. Few would question the goals of economic and social justice or their fashionable surrogate, sustainable development, but the premise that a new economic order would, alone, solve the biodiversity crisis (*50*) is suspect. The North American, let alone the Costa Rican experience (*4*), suggests that social justice and other progressive changes cannot protect biological diversity in the face of rapidly changing economic conditions including the internationalization of markets, increasing human numbers, the loss of cultural and ecological traditions, not to mention ethnic and religious conflicts. Even wealthy countries such as the United States and Canada justify the removal of the last remnants of ancient forests on the grounds of economic necessity; attempts to save that remaining 15% of original forests in the Pacific Northwest have yet to prove successful (*18*). In addition, corruption and bureaucratic inefficiency appear to be virtually indelible.

Policy implementation. There are many reasons for the inability of modern states to enforce laws and implement conservation policies, especially policies that require short-term sacrifices for the sake of long-term benefits. For example, the setting aside and long-term protection of land from the national estate is improbable in societies with many poor or landless people, powerful oligarchies, or corruptible judges and bureaucrats.

In countries where adequate resources are lacking for the protection and management of protected areas, even relatively secure reserves are subject to the removal of trees and to the poaching of game. Most poor nations simply lack the resources to preserve biotic diversity in situ (*51*). Such attrition is frequent during "normal" times (*52*), but during periods of social unrest, the loss of biodiversity can be catastrophic (*53*).

Many conservation and development projects are destined to fail in a statistical sense, given their unstable social or political contexts. Wars and the breakdown of civil administration can undermine decades of successful policy implementation. In Africa, recent wars in Ethiopia, Sudan, Liberia, Libya, Morocco, Somalia, South Africa, Zimbabwe, Uganda, Chad, Angola, Mozambique, Rwanda, Burundi, and other countries have led to the partial or complete collapse of nature reserves, the destruction of habitat, and the local extinction of endangered species (*53*). The frequency of events such as wars should be built into the planning processes of responsible agencies and organizations. This is not to say that we should abandon reserves in regions where civil chaos is frequent. Rather, expectations and policies must be tuned to appropriate distributional parameters—for example, to the mean and variance of persistence times of protected areas in similar situations and to the kinds of damage that protected areas are likely to suffer, including the killing of most large animals. The lower the mean and the higher the variance, the greater the emphasis there must be on redundancy, on alternative approaches, and on backup, ex situ projects. It would be prudent, in other words, to think of nature reserves as ephemeral islands, and to plan accordingly.

The human condition is dynamic and unpredictable and will remain so for at least a century, if for no other reasons than the momentum of the population explosion and the unsatisfactory economic and social status for billions of people during the 21st century. The "biotic condition," therefore, will also be tenuous during this interval. Fortunately, conservationists have an increasing number of tools with which to deal with the crisis.

Tactics and Conflicts

The eight paths to biotic survival. What tools are available to protect living nature from humanity? Table 2 presents a brief survey of eight conservation tactics or systems (*5*). The tactics are defined roughly in order of least to most artificial or intrusive.

1) *In situ* refers to those conservation systems based on bounded wild areas with relatively little human disturbance; it includes most protected areas, from wilderness parks to the core areas of biosphere reserves (*54*). Persistence may depend to some extent on the economic benefits, as generated, for example, by tourism, but protected areas tend to degrade, even in the best of circumstances, and few, if any are large enough to maintain viable populations of large predators and omnivores without ex situ supplementation (*16, 19, 26, 55*).

2) *Inter situ* refers to conservation systems or activities in regions where native species still persist, but which are outside the boundaries of established protected areas. Most of the lands belonging to this category are nonarable; typically, they are relatively infertile, cold, steep, rocky, or arid. In the United States, most such regions are administered by the Bureau of Land Management and the U.S. Forest Service.

3) *Extractive reserves* permit certain kinds of resource harvesting on a (theoretically) sustainable basis. Examples include rubber tapping, the collection of edible fruits and nuts, thatch grasses, and, perhaps, even limited logging and hunting. Sustainability of such practices, however, depends on a low population density, a stable economy, and careful management (*56*). In practice there may be little difference between extractive reserves and inter situ projects, except that the latter are more circumscribed.

4) *Ecological restoration projects* refers to intensive management activities intended to increase species richness or productivity in degraded habitats. Among the necessary conditions for such activities are political and institutional stability.

5) *Zooparks* refers to facilities in secure locations where a mix of local and exogenous species can be maintained under seminatural conditions—in other words, sanctuaries for sensitive species of diverse provenance (*57*). The assumptions underlying the establishment of such reserves are that protected areas, in many places, are not viable for social

Table 2. The relative potential significance of eight different conservation systems for the protection and maintenance of natural biological diversity. The "0" indicates little or no role; "X, XX, and XXX" indicate low, moderate, and high significance, respectively. The order of the systems does not imply a ranking of value.

Targets of conservation	Conservation system							
	In situ	Inter situ	Extractive reserves	Restoration projects	Zooparks	Agroecosystems & agroforestry	Living ex situ	Suspended ex situ
Entire systems (ecosystems)								
Processes or functions	XXX	XX	XX	XX	XX	X	0	0
Biosocial (traditional human uses)	X	XX	XXX	XX	X	X	0	0
Biogeographic assemblages	XXX	XX	XX	X	XX	0	0	0
Indigenous and endemic species	XXX	XX	XX	X	XX	X	XX	X
Local populations of species	XXX	XX	XX	X	XX	X	X	X
Genetic variation within species								
Wild relatives of domesticates	XXX	XX	XX	X	X	X	XXX	XX
Traditional domesticated varieties	X	X	X	0	X	XX	X	XXX
Noneconomic genetic variation	XXX	XX	XX	X	X	0	X	X
Ownership	Public & private	Private & public	Public & private	Private & public	Private	Private	Private & public	Private & public

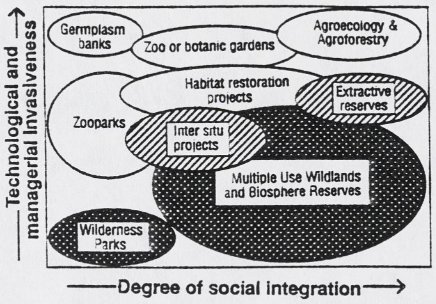

Fig. 4. Descriptive distribution of conservation tactics according to the degree of social integration at the local level, and the degree of technological input or management intensity. Shading indicates relative degree of human interference with natural processes; darker shades indicate less interference. The positions shown for each tactic are meant to suggest the center of the probable zone of action for the tactic. The term "Biosphere Reserves" refers to multiple use, production-oriented projects, with a relatively sacrosanct core protected area.

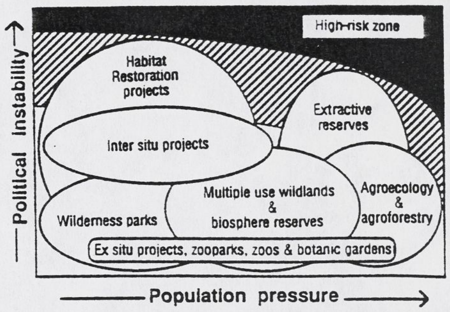

Fig. 5. Prescriptive distribution of conservation tactics based on the probability of increasing population pressure and the likelihood of political instability or violent conflicts. Backup, ex situ facilities are placed in relatively secure, politically stable locations.

or political reasons and the inevitability of highly recombined biotic communities in the future given current rates of species introductions (*58*). This category differs from in situ reserves because of the conscious introductions of target species.

6) *Agroecosystems and agroforestry projects* are highly managed, production-oriented systems with a wide range of dependence on artificial chemical and energy inputs (*59*). The number of native species that can survive in such systems is highly variable, depending mostly on the proximity of garden, farm, and plantation to wildlands, the use of artificial chemical inputs, and the tolerance of farmers to wildlife (*60*).

In addition to zooparks, there are two kinds of ex situ tactics or backup systems (*14*). These are essential where particular reserves are likely to fail or lose significant numbers of their species.

7) *Living ex situ* programs refers to botanical gardens, zoos, aquaria, and similar institutions that maintain and propagate living organisms for noncommercial (education, research, conservation) purposes in a highly controlled, usually urban, context.

8) *Suspended ex situ* programs are completely artificial; living material is metabolically slowed or arrested. Among these projects are germplasm storage facilities such as seed banks, tissue culture collections, and cryopreserved collections of gametes, zygotes, and embryos.

As shown in Table 2, this typology of tactics manifests a current trend—the privatization of conservation. For many reasons, nonprofit groups and individuals increasingly are complementing if not supplanting government agencies in protecting biodiversity. Private zoos, botanical gardens, and others are taking responsibility for the captive propagation of endangered species. Responsibility for the restoration of degraded forest, pastures, and farmlands on both public and private lands is being assumed by private groups. Organizations like The Nature Conservancy and Conservation International are acquiring new sites for protected areas (*61*), though governments are usually the ultimate owners.

Social Context and the Debate over Tactics

Current discussions have tended to oversimplify the diversity in conservation approaches by exaggerating the differences between the so-called species approaches and ecosystem approaches. The former emphasizes the protection, both in situ and ex situ, of endangered, often charismatic vertebrates, whereas the objective of the latter is to set aside and manage natural areas based on systems of landscape classification that will capture as much species and ecological diversity as possible (*62*). Critics of species-level approaches have emphasized the shortcomings of the Endangered Species Act and point out that most of the federal dollars are directed at a few birds and mammals (*62*). Some of these critics argue that success in captive breeding and cryopreservation will lead to complacency about the need for more and better protected areas. Supporters of endangered species might counter that if it were not for the charismatic species, the public appeal of conservation would be much less, that endangered species justify many of the larger protected areas in the United States and elsewhere, and that endangered species legislation is providing the economic leverage to bring developers and government agencies into negotiations about the preservation of large areas of habitat for general biodiversity conservation in the United States (*63*).

Such adversarial discussions, however, often ignore social context. As shown in Fig. 4, conservation tactics can be ranked according to the degree each is integrated into the local human community and the degree that each is dependent on artificial (technological) means and invasive management practices. Implicit is idea that different tactics require different degrees of social and technical sophistication.

A more prescriptive classification is shown in Fig. 5. It distributes the tactics in a plane of human population pressure and political stability. It is based on the untested assertion that the persistence of conservation projects, particularly protected areas, is related to the frequency and degree of political unrest and the rate of population growth. The combination of the two figures suggests that the choice of tactics should be influenced by the probable impact of demographic, economic, and social conditions as discussed above. For example, ex situ tactics are prescribed where political instability is frequent and where population pressure is building.

Much of the debate in the United States over approach and tactics stems from uncertainty and bias about landscape and geography, the importance of socioeconomic conditions and the stability of political structures, confidence in new legislative and legal remedies, and the identity of target organisms. For example, conservationists with experience in the species-rich tropics—where infrastructure is fragile at best, episodes of social chaos inevitable, human populations are doubling every few decades, laws are ignored, and hunting of rare animals and deforestation are a way of subsisting—should support a pluralistic approach that includes ex situ backup for protected areas. On the other hand, those with experience in wealthy, stable, temperate zone regions—where most species have wide geographic ranges and where there exists extensive areas of low productivity, government-owned lands—are more likely to promote systems of protected areas linked by corridors in multiple use zones that can be managed for conservation and sustainable forms of exploitation (*64*). They will also have more faith in legislative remedies and law enforcement. Figure 5 illustrates this tactical pluralism.

Conclusions

Today, the conservation of biodiversity is virtually equivalent to the ex situ protection of wildlands. In the future, however, such reserves will come to be seen actuarially, their life times dependent on many biogeographic, social, and political factors. Unless a much denser and more secure network of protected areas is established soon, the importance of less appealing alternatives will be greater than conservationists would wish.

This awareness has led some observers to call for a greater emphasis on adjunctive approaches, including inter situ projects—the management of wildlife in nonarable lands outside of traditional reserves (*65*). Though appropriate in certain places, these lands are not immune to overexploitation, desertification, and to other forms of abuse, as the recent history of Tibet, the Sahel of Africa, and the American Southwest have shown. The inter situ tactic is an important backup, however, especially in socially and demographically stable nations and regions. The point is that every tactic has its limitations; sole reliance, for instance, on ecological restoration or on cryopreservation technologies would be premature, if not immoral, because these technologies could protect only a tiny fraction of species diversity for the foreseeable future, especially in tropical seas and forests.

Progress in conservation is hampered by the lack of a clearly articulated public policy on biodiversity. The United States and many other countries lack a coherent conservation strategy. In part, this may stem from confusion about tactics, as discussed above. The United States should join the nations that have developed a national conservation or biodiversity strategy. There is also a need for new institutions such as a National Institutes of the Environment (similar to the National Institutes of Health) to provide intellectual leadership and sustainable funding for planning and research in biodiversity. In addition, a high level review of federal agencies is necessary so that either the authority for the protection of biodiversity is vested in a new agency with clear directives, or the organic acts (if any) of the agencies should be restructured, making conservation a prime directive of the U.S. Forest Service, the Bureau of Land Management, and the National Wildlife Reserve System.

Everywhere, nature reserves must be defended and bolstered by social experimentation in "sustainability." But there is too much at risk to gamble on any one social ideology, theory, or approach. All human institutions are transient expedients, and the conservation systems that are fashionable today will certainly undergo many changes in the next century. Opportunism and tolerance must be the watchwords of the science, the politics, and the art of nature protection (*66*). The issue, therefore, is not the "failure" of conservation; it is whether it can stay the course. During the construction of cathedrals in the Middle Ages, planners and artisans were not dismayed that "success" might require centuries. Like those workers, conservation scientists and practitioners must accommodate their objectives to the social complexity and temporal scale of their enterprise (*67*).

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SOCIETY FOR CONSERVATION BIOLOGY NEWSLETTER

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R. Bolinke

THE PRESIDENT'S COLUMN

Why do we want to conserve biodiversity anyway?

One might think that the subject of this essay is superfluous in the SCB newsletter, but I am quickly discovering that it is not. In discussions with dozens of people in all walks of life I have found a rather startling naivete on what biodiversity is, why it is important, and why we are concerned about it. Most of us are comfortably ensconced in academic or other environments where it is a sine qua non that biodiversity conservation is good. It comes as a rather rude surprise to find out how many people in the world are ignorant of, indifferent toward, or opposed to the conservation of biodiversity. Among these are many elected officials, some state and federal agency employees, most people working in the extractive industries, a goodly number of farmers and ranchers, a few environmentalists, and a generous share of the public at large. In short, we will have to "sell" biodiversity to many constituencies before we can succeed in conserving it.

We have tried a number of sales pitches over the past few years, and some have been more successful than others. Here are four of them.

1. *It's the law.* While clearly true (in the United States, 31 pieces of federal legislation mandating the conservation of biodiversity have been passed by Congress, and many states have similar laws), this argument has won few converts. In the western U.S. in particular, many groups regard biodiversity conservation as yet another example of federal interventionism designed to diminish their "rights" or means of livelihood. This argument has sometimes been useful, however, in extracting cooperation from persons accustomed to dealing with federal and state environmental regulations.

2. *Other species and natural communities have intrinsic value and hence a right to exist.* While I would be the first to admit that the development of less anthropocentric philosophies is critical for the world's future, few people who are not already converted have been swayed by this argument. Even at best, intrinsic value discussions seem to be much more persuasive when dealing with organisms that are cute and cuddly or bright and colorful rather than with comparatively drab native minnows or obscure plants. Educating the next generation is the best way to make intrinsic value arguments convincing. At present, if the first question someone asks about an endangered species is "What good is it?" it is probably best to move on to a different line of argument.

3. *Biodiversity conservation makes good economic sense.* This approach seems to have been more successful than others, although it too meets with its share of skepticism. Here is the argument in brief.

a. A region's natural resources are its capital; natural resources are both abiotic (e.g. water, minerals) and biotic.

b. Biological resources consist of natural and semi-natural ecosystems, the species found in these ecosystems, and the genetic information that these species contain. These resources are maintained by a variety of ecological and evolutionary processes, and the resources plus the processes that maintain them are sometimes referred to as *biodiversity*.

c. Biodiversity not only provides goods, such as forage for livestock and fish and wildlife for harvest or enjoyment, but also services, such as control of hydrologic cycles, detoxification of waste, and generation of soil. (Most people understand the goods part; few are aware of the services. Many are surprised to realize, for example, that events occurring in distant forest ecosystems can determine the quantity and quality of water that comes out of their faucets.)

d. Many human activities, such as management focused on single-species or commodity production, have led, often unwittingly, to ecosystem degradation. Highly degraded ecosystems are not effective producers of either goods or services, and once ecosystems reach this state their restoration is slow and costly at best and impossible at worst. Thus, conservation and economics are inextricably linked. The restoration of degraded ecosystems is going to be a huge cost that we will pass on to future generations if decisive action is not taken now. The conservation of biodiversity is not necessarily incompatible with other land uses, although some compromises will be required.

4. *Biodiversity conservation may help get the government off your back.* This line of argument is the most pragmatic of all, but it has caught many people's attention. Its two components are

a. One of the major indicators of widespread ecosystem degradation is the ever-increasing list of endangered, threatened, and candidate species. Recent evidence suggests that many species that are still common will soon join the queue because a substantial proportion lack the dispersal capability to exist in highly fragmented landscapes. Every time the Endangered Species Act or comparable legislation is invoked, additional governmental restrictions result.

b. Biodiversity conservation, by helping to reverse ecosystem degradation, will result in far fewer listings under the Endangered Species Act.

It is critical for us to disentangle knowledge of the importance of biodiversity conservation from the practice of conservation biology. Every conservation biologist should be well-versed in these and similar arguments and must be prepared to present them on a moment's notice; lack of preparedness can easily be interpreted as lack of commitment. Of course, once people are convinced that biodiversity conservation really is a good idea, it is also important to be able to demonstrate convincingly how conservation biology can offer much useful guidance in this regard.

Peter F. Brussard

There is a false paradox about conservation programs and time scale. A critic might ask, "Why the haste if conservation projects must last centuries?" The problem is the that the current rate of biotic destruction demands immediate actions. This is not inconsistent with the objective that they persist a long time.
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An Evolutionary Basis for Conservation Strategies

Terry L. Erwin

Conservation strategies have been remarkably anthropocentric from their inception in the Middle Ages to the present (*1, 2*). During dynastic and feudal times, parts of kingdoms were set aside as hunting grounds for the aristocracy, thus preserving everything that dwelled therein. This, plus severe natural and cultural control of human populations resulted in environmental protection for centuries. Today, with a burgeoning and expanding human population of 5.3 billion, no more than 4500 areas are protected globally (*1*); that is equivalent to a mere 3.2% of our planet's landmass. National parks, wildlife refuges, biosphere reserves, military reserves, Indian reservations, and other forms of legally protected areas have been established for aesthetic, political, or practical purposes in the last 150 years. Many reserves in less-developed nations are paper parks only; many in the more developed are lamentably endangered by touristic herds, and certain wilderness parks are threatened by short-sighted national energy policies.

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Today, conservation strategy is based on a perceived impending loss of biodiversity due to tropical deforestation or disappearing habitats where populations of "interesting" species, subspecies, or even varieties (especially in temperate areas) reside. Campaigns usually focus on loss of potentially useful resources, such as plants with pharmaceutical properties or large animals that capture human interest. In practice, this results in saving fauna and flora in a few "available" acres where a well-known target taxon lives. Science has been too slow in providing inventory data to do much more; thus, what should be a major collective effort between conservation and science is often nonexistent, or in some cases, discord.

In the past 3 billion years, more species and their natural assemblies with their particular interactions have come and gone than are now present on Earth (*3*). One fact of evolution is that species go extinct, and others come into existence. Today, because of unprecedented human impact, species are increasingly going extinct and the speciation process, which creates future biodiversity, is being severely pressured through the removal of contiguous related biotic habitats. The pattern of continental habitats, often vast biomes, is being reduced to one of scattered island-like habitats and, just as on real islands, major extinctions are destined to occur. If this disruption of natural systems continues into the 21st century, we can expect the evolutionary process as we know it to become degraded and retarded.

There is no unified scientific method behind conservation strategy that addresses the nature and quantity of biodiversity, nor what it means environmentally either to save it or lose it outside direct human interest. In fact, there is little altruism or science in the fight to save the rain forest, the spotted owl, or the Antioch blue butterfly. Rather, politics and economics weigh heavily on most decisions. It seems that degradation and conversion of the environment is proceeding so rapidly that getting something preserved—anything at all—is acceptable regardless of the yardstick. Worst of all is that legitimate arguments within the scientific and conservation communities allow decision-makers an out in politically difficult choices. In order to supplement positive conservation practices and provide an alternative to negative ones, an effort to establish a sound scientific underpinning must be made. Scientific rationale may transcend cultural changes through time, whereas economic and political grounds certainly will not.

What is biodiversity? Is it important, and if so, important to what? Is it possible to separate contemporary human needs from what is really necessary for the long-term environmental health of the planet? How can we hope to manage 30 or more million species? Given the myriad of societal demands and an ever-increasing population, what can realistically be achieved even if a global effort is sustained in environmental management? Should conservation strategy be scientifically or culturally based? These and others are the tough questions with which political systems must deal. For scientists, the question is what can we provide from our science that will help generate a long-term, transcultural foundation on which conservation strategy can be based?

Biodiversity can be equated with species richness, that is the number of species, plus the richness of activity each species undergoes during its existence through events in the life of its members, plus the nonphenotypic expression of its genome. Biodiversity evolves through numerous processes that vary from locality to locality, habitat to habitat. Species richness at a site is a readily observable index of the number of interactions among and between species and how these species are grouped as a living unit at that site. A species richness index then is a reasonable and knowable tool that can be used in setting policy and making decisions about biotic conservation and management. To understand the significance of a biodiversity index across geography, one needs context. Relationships between species and a knowledge of lineages to

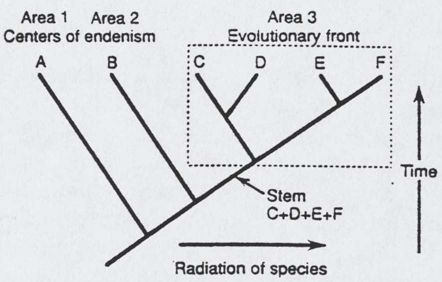

Fig. 1. Simple cladogram of seven species in a monophyletic lineage. More complex lineages may have more than one evolutionary front.

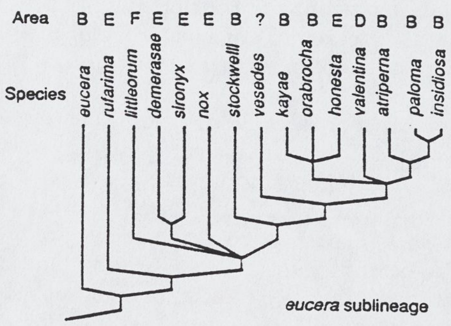

Fig. 2. Cladogram of the *eucera* sublineage of the carabid beetle genus *Agra* (*9*).

which they belong provide that context.

Radiation of lineages of organisms occurring on both continents and islands proceeds stepwise and requires contiguous habitats of various kinds through which sequences of phylogenetically related species pass as the lineage to which they belong rises to dominance (within the context of the occupied habitat) and ebbs to extinction (*4, 5*). Centers of endemism, or relict occurrences of organisms, are the last remaining footholds of past radiations. Elsewhere these endemic organisms have been replaced by better adapted lineages to an ever-changing contemporary environment. This model taken to its extreme, given current trends, indicates that within a few hundred years this planet will have little more than lineages of domestic weeds, flies, cockroaches, and starlings, evolving to fill a converted and mostly desertified environment left in the wake of nonenvironmentally adaptive human cultural evolution.

What should we know to aid in countering the planet's impending biotic destruction? Assuming that it is the species radiation part of the evolutionary process, the generator of biodiversity, which is endangered, and that is what we (altruistically) decide to protect through scientifically based choices rather than cultural ones, we need to know where lineages (not individual species) originate innovations in their evolution and how these become distributed over some part of the planet. The disciplines involved to achieve this are phylogenetics and biogeography, together referred to as systematics. We need to use this science to tell us where the critical areas are that need sound environmental management—that is, where we need to protect the active processes of contemporary evolution. The most powerful tool to emerge during the past 20 years as a robust and comparative science, with both practitioners and theoreticians, is phylogenetics (*6, 7*) and its methods and applications (*8, 9*). Phylogenetics is well suited to provide predictions of as yet unobserved qualities that are directly applicable to conservation decision-making (*10*) and because its tools are now computer-based it can be applied in a short time to many groups for detecting congruence in patterns of occurrence of radiating lineages (*9*). Site congruence, which can be mapped easily, of many evolving lineages can then become the target of conservation activities.

A cladogram illustrating the hypothetical phylogenetic relationships among seven known species that make up a monophyletic lineage of organisms is shown in Fig. 1. According to such an analysis, species A and B have not demonstrated radiation—that is, the ability to evolve into a more broadly adaptive and widespread lineage through time. Both are found to be geographically restricted endemic forms (relics) occupying small areas. Current conservation strategy places highest priority for protection on such areas as 1 and 2 (*11*). Endemic forms such as A and B are often unusual or rare, and even interesting to many scientists (*12*), but they are predictably on their way to extinction. These forms carry information about past evolutionary flourishes; they are important to protect, but they are only half the picture. The relatively more recent sublineage in Fig. 1 (stem C + D + E + F) is where phylogenetic theory predicts radiation and dynamic changes in taxa are occurring today and will occur in the future. Species such as C, D, E, and F are sometimes widespread and may even be regarded as "weedy" species, but does that make them less important? Their stem has become the multispecies sublineage that holds the most promise for continued evolution of this line of biodiversity under natural conditions. For example, in the *eucera* sublineage of the carabid beetle genus *Agra* (*9*) (Fig. 2), current interest would focus on areas D and F, each of which contains a relatively primitive and rare species. The cladogram (Fig. 2) shows that areas B and E contain both recent radiation and older species of the sublineage. If the *eucera* sublineage were something of general conservation interest, then the investment for protection would be better put into areas B and E to maximize

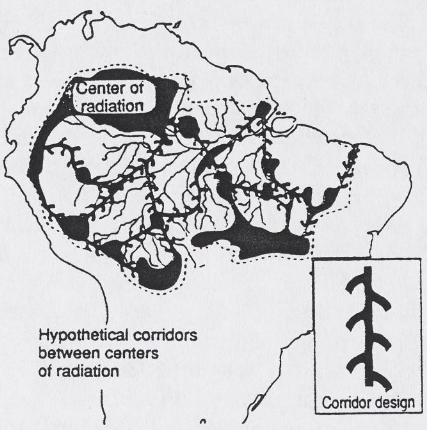

Fig. 3. Future corridors of ecological reconstruction between hypothetical centers of radiation—for example, in the Amazon Basin, to allow species movements and radiation. Inset is a design for a corridor that maximizes soil and habitat types in small areas.

salvaging this kind of beetle diversity now and in the future. Vane-Wright *et al.* (*13*) provide a novel index for cladogram analysis that needs careful testing in its application to making choices in conservation of taxic diversity. Congruence across many groups with their method may be the best way to find centers of radiation for conservation purposes.

Conservation strategy should incorporate methods to detect such contemporary evolution for the good of future maximum biodiversity. Conservation of only an accumulation of mostly nonradiating endemic taxa, the current conservation strategy (*11*), is like saving living fossils, something of human interest, but perhaps not beneficial to the protection of evolutionary processes and environmental systems that will generate future biodiversity.

Through analyses of diverse groups and detection of congruent patterns among radiating lineages (*8*), evolutionary fronts (centers of radiation) can be detected and targeted for long-term protection. Site protection and future ecological reconstruction of natural corridors (Fig. 3) between important centers will be essential to allow continued species radiation because climatic shifts may displace species' ranges (in isolated parks great extinction will occur); evolution proceeds from centers of radiation outward through sequences of contiguous habitats latitudinally and altitudinally and there become disrupted from time to time allowing speciation.

Evolutionarily dynamic lineages today create future biodiversity. Such lineages are the cornerstone of natural environmental health. Science has the philosophy and tools to detect these lineages through phylogenetic systematics. Conservation strategy can use the patterns detected in cladistic studies to defend contemporary centers of radiation from destruction on the premise that today's maximum biodiversity, as well as tomorrow's, are in and stem from such centers. Acceptance of a nonhuman yardstick to measure environmental health—that is, evolutionary processes—and implementation of a scientific approach in conservation policies will provide a strategy to achieve a lasting stability for global environmental health because the basis for conservation will not be tied to the whims of human culture. The goal of conservation strategy should be the protection of future maximum biodiversity as well as preservation of contemporary species of human interest.

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Balancing Species Preservation and Economic Considerations

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HOW MUCH IS A SPECIES WORTH? WE GENERALLY TAKE AN anthropocentric view of that question. The species *Homo sapiens*, as judged by the lives and well-being of individuals, is infinitely precious in our public ethic. A tiny arachnid, found only in the sands of Suvarov Islands, isolated in the mid-Pacific, is likely to get a much lower rating. The question becomes, "What is the value of a given species to human society?" Once the term "value" is introduced, the question moves to economics and ethics, both of which use that construct, but in very different senses. From a narrow economics point of view, we need a monetary metric of a species value to balance benefits against costs of preservations (*1*). Viewed from environmental ethics no such direct measure is possible (*2*). These considerations apply to ecosystems as well as to individual taxa. We are often left trying to balance the "good" of ethics with the "goods" of economics.

Some conservationists have argued for the virtue of the preservation of almost all species (*3*). There are techno-optimists who downplay the species problems (*4*). Extremist advocates of artificial intelligence envision a silicon chip–based "life" to succeed carbon-based humans (*5*). Some traditional economists might argue that the amount we are collectively willing to expend to preserve a species is an appropriate utility measure. But traditional theory does not deal effectively with goods not exchanged in organized markets. Free air and water pollution are examples of this approach. One senses that there has been far too little dialogue between environmental biology and economics.

The National Academy Forum on Biodiversity (*3*) devotes 30 of its 500 pages to economic issues, and the newly formed Society for Ecological Economics has begun to approach value problems. But one senses that there is not a full engagement of either of the contributing disciplines. Economics students are not required to study biology, and the curriculum of ecologists does not usually include economics. As noted in a recent business publication, "Environmental economics has been relegated unfairly to the mar-

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Many environmental battles are being fought on these grounds.

There is a school of economic analysis (*10, 11*) that maintains that environmentally unsound practices are often economically unsound and involve governments fostering habitat destruction to protect politically influential industries. This leads to (*11*) "the use of limited natural resources at practically no cost." A number of examples are given (*10*) from the logging industry in the United States. The author maintains that in many cases the government is in fact subsidizing the clear-cutting of forests to produce a product that would be noncompetitive in the market without the subsidy. This is the reverse of the role a government should play in dealing with public goods.

What becomes clear is that it is not true that a species is a species is a species. The debate about preservation and management versus letting nature take its course must be argued for each taxon and habitat in some detail based on an understood and agreed upon way of assigning values. If preserving a species is to be used as a cover statement for preserving a habitat, it would be better to get the actual reasons up front so they can be debated on merits. Except in those very few cases where cost and benefit have calculable monetary values, conversion factors will have to be developed in terms of more abstract benefits. As has been pointed out by Baden (*12*), "not all values can be denominated on a spreadsheet."

It is necessary to stress that none of the trade-offs necessary to establish the relations between different value systems can be accomplished until biologists, economists, and technologists are willing and able to carry out discussions. A rational approach to problems demands this kind of communication. One would envision that the recently proposed National Institute for the Environment would be a locus for this activity, which at present lacks a home.

At the beginning of this century, humankind inherited a great diversity of biota. The industrial revolution inevitably compromised habitats and led to large-scale extinctions. We have reached a stage where there is general agreement that ecosystems, including the global ecosystem, must be managed (*13*). This requires, at the very least, more effort devoted toward an improved understanding of ecological theory. It also urgently requires some national and international consensus as to the goals of that management. Public goods are clearly the province of governments.

We would be remiss not to repeat the assertion that as human population goes up, biological species diversity goes down. We might be able to moderate the rate of decline, but we cannot fend off the inevitable. As species number goes down, we might, of course, change our valuation system and subsequent responses; they are, after all, cultural, not metaphysical. The answer to "How much is a species worth?" is "What kind of world do you want to live in?"

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Extinctions: A Paleontological Perspective

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THE FOSSIL RECORD IS RICH IN EXTINCTION: THE STAGGERing diversity of the present-day biota (*1*) represents a minute fraction of the taxonomic and morphologic variety that has populated the earth since the explosive diversification of multicellular organisms at the beginning of the Phanerozoic. Compilation and statistical analysis of temporal ranges of fossil taxa have verified that extinction intensities per unit time have varied widely, with a continuum from low to high intensities. Background extinction is recognized operationally as the troughs between extinction maxima in time series, and may involve the loss of only a few species. At higher intensities, extinctions may affect only a narrow subset of species (as in the late Pleistocene megafaunal extinction), or may be taxonomically and geographically pervasive (as in the mass extinctions as currently defined) (*2–7*). Paleontologists have learned much about the timing, magnitude, selectivity, and recovery patterns of the major extinction events (*8*), but the implications of these data for present biodiversity are still not fully understood. The fossil record is, however, our only direct source of information on how biological systems respond to large-scale perturbations and thus can provide important insights into potential outcomes if habitat destruction or climate change proceeds unchecked (*9, 10*).

The most basic observation is simply that mass extinctions have happened: irreversible biotic upheavals have occurred repeatedly in the geological past. Marine and terrestrial biotas are not infinitely resilient, and certain environmental stresses can push them beyond their limits (*11*). This basic message derives not only from the fossil record of the five major mass extinctions of the Phanerozoic, but from smaller events like the end-Cenomanian and end-Eocene events (Table 1), and regional extinctions like the Pliocene loss of more than 50% of northeastern Atlantic and 75% of northwestern Atlantic bivalve species (*12*). The major mass extinctions have apparently mediated faunal replacements that were once attributed to a more classically Darwinian competitive process (*13, 14*): dominant groups decline or disappear and previously unimportant taxa rise to prominence in the aftermath, as seen in the successive reef biotas of the Phanerozoic (*15, 16*) and the successive terrestrial vertebrate dynasties from mammal-like reptiles to dinosaurs to mammals (*13*). Terrestrial plants have sometimes been described as exempt from ancient mass extinctions (*17*), but this is true only at the highest taxonomic levels. Detailed work on species and genera, for example, suggests that the end-Cretaceous extinction removed more than 50% of plant species and may have played a pivotal role in structuring the Cenozoic flora, at least in the Northern Hemisphere (*18*).

Survival of species or lineages during mass extinctions is not strictly random, but it is not necessarily closely tied to success during times of normal background extinction. Analyses of selectivity during mass extinctions are still scarce, and patterns emerge more

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Table 1. Extinction intensities at the genus and species level for the five major mass extinctions of the Phanerozoic and selected smaller post-Paleozoic extinction events. Generic values are calculated empirically from the marine fossil record (*3*); species loss inferred by rarefaction from generic data (*3, 65*). Age values from Harland *et al.* (*42*).

Extinction	Age ($\times 10^6$ years)	Genera (%)	Species (%)
Late Eocene (Priabonian)	35.4	15	35 ± 8
End-Cretaceous (Maastrichtian)	65.0	47	76 ± 5
Late Cenomanian	90.4	26	53 ± 7
End-Jurassic (Tithonian)	145.6	21	45 ± 7.5
Pliensbachian	187.0	26	53 ± 7
Late Triassic (Norian)	208.0	47	76 ± 5
Late Permian	245.0	84	96 ± 2
Late Devonian (Frasnian)	367.0	55	82 ± 3.5
Late Ordovician (Ashgillian)	439.0	61	85 ± 3

clearly at lower taxonomic levels than at high ones, but some generalizations can be drawn. Among terrestrial vertebrates, for example, large-bodied lineages appear to suffer more severely than small-bodied forms {witness the end-Cretaceous dinosaurs [though juvenile and small adult forms also vanished (*19*)] and the end-Pleistocene megafauna (vertebrates over 44 kg)}; this makes biological sense, in terms of such factors as expected population sizes and densities (low), home range requirements (large), generation times (long), and trophic requirements (large) (*20*). The ecological consequences of the removal of these large vertebrates are only beginning to be explored, and the exploration requires reciprocal neontological-paleontological study, but may be far-reaching. In part on the basis of ecological research in Africa, the one continent that retains much of its Pleistocene megafauna, Owen-Smith (*21*) suggests that the end-Pleistocene extermination in North America of the species most attractive as human prey, such as mastodon and mammoth, would have brought extensive vegetational changes that in turn would explain the concomitant disappearance of so many other vertebrates. Such cascading ecological effects have long been suspected for the major mass extinctions [for example, the probable collapse of marine food chains with the end-Cretaceous phytoplankton crisis (*22*)], and may provide a useful model for the potential consequences for local or total extermination of present-day elephants and some of the other African megaherbivores (*23*). Controlled ecological experiments are still the most powerful way to predict responses of particular communities to species removals (*24*), but this approach would be particularly valuable if designed around removal of species likely on demographic or paleobiological grounds to be most extinction-prone.

Among marine invertebrates, where the fossil record is more completely known and more readily quantified (*25*), at least one strong generalization has emerged: widespread genera preferentially survive mass extinctions, whereas geographically restricted genera are particularly vulnerable (*14, 26–29*); during background extinction geographical range more demonstrably plays a role at the species level (*30*). Some factors that contributed to genus survival during background times, such as species richness, were ineffective during the end-Cretaceous mass extinction, so that molluscan and echinoderm taxa were lost that ordinarily were extinction-resistant (*14, 26, 31*); the same holds for early Paleozoic trilobites (*28*), late Devonian corals (*32*), and Paleozoic ammonoids (*33*) but not, apparently, for end-Permian gastropods (*29*). Major extinction events also preferentially or indifferently removed taxa normally at low risk among Paleozoic bryozoans (*34*), Late Cenozoic Foraminifera (*35*), and Late Cenozoic bivalves (*35*). Evidence is thus accumulating that taxa and morphologies may have been lost not because they were poorly adapted by the standards of background processes, but because they occurred in lineages lacking the environmental tolerances or geographic distributions necessary for surviving the mass extinction.

The paleontological data, then, corroborate suggestions (*9, 10*) that present-day perturbations are likely to impinge most heavily on rare, geographically restricted species, and can be indifferent to adaptations honed by prolonged intervals of natural selection under background extinction. In the face of ongoing habitat alteration and fragmentation, this implies a biota increasingly enriched in widespread, weedy species—rats, ragweed, and cockroaches—relative to the larger numbers of species that are more vulnerable and potentially more useful to humans as food, medicines, and genetic resources. However, we have little means of translating paleontological data into predicted rates or patterns of species loss for any given present-day locality or region. Data are needed on living species that allow direct comparison with the fossil record. For example, frequency distributions of geographic ranges for local faunas and floras would provide a framework for inferring the most vulnerable taxa, and for assessing possible impacts of losses at the more extinction-prone end of the geographic range spectrum. Such an approach will, of course, provide only a first approximation of extinction probability; some species, for example, are widespread but have narrow requirements (*36*), such as a herbivore dependent on a complex of geographically restricted (and thus extinction-prone) plant species. Nevertheless, the high rate of habitat disturbance or fragmentation, particularly in the tropics, lends urgency to the development of efficient approaches to estimating potential biotic consequences.

The fossil record also suggests that tropical biotas are the most vulnerable to extinction (*37*). The general impression, however, needs to be more fully explored: few data are available for terrestrial organisms, and the underlying marine data derive mainly from the striking demise of reef communities at each of the major mass extinctions (*15, 16*), combined with some evidence for relatively low extinction intensities at high latitudes (*38*). Whether this boom-and-bust history reflects the vulnerability of the tropical marine biota in general, the vulnerability of the reef community in particular, or a chain of events put in motion by the extinction of geographically restricted species, as elsewhere on the globe, is not known (*14*). Reef biotas survived Pleistocene climate and sea-level fluctuations with few losses (*39*), but this may be an unreliable model for the present-day situation. Pleistocene reef species depended not upon withstanding in situ stresses but on shifting to or persisting in benign refugia (*39, 40*) now becoming increasingly scarce as human activities impinge on these environments.

Biotic recoveries after mass extinctions are geologically rapid but immensely prolonged on human time scales. New reef communities are not recognizable until 5 million to 10 million years after extinction events (*15*), and Talent (*16*) argues that the re-invasion—and re-invention—of these habitats postdates by millions of years the slackening of the environmental perturbations associated with the demise of the preceding community. Further testing is needed, but the delay evidently reflects constraints on the evolution of species or assembly of communities capable of occupying these habitats rather than on continuing environmental stresses. Similarly, marine bivalves show episodes of accelerated diversification in the wake of mass extinctions, with recovery to pre-extinction levels of generic diversity requiring at least 10 million years (*41*). Whatever the exact magnitude of present-day diversity losses, rebounds in the fossil record suggest that they will not be recouped in the next thousand years, even in the absence of further disturbance. Comparative analysis of geologic intervals with intense turnover but modest drops in standing diversity might reveal taxon-specific or habitat-specific thresholds below which "instantaneous recoveries" are not possible. Such estimates could be used to weigh the risk of incurring truly long-term consequences under alternative management schemes.

Comparisons between present conditions and the fossil record are severely hindered by problems of temporal and taxonomic scale, and by a basic nonequivalence between the kinds of data available for the two systems. Reliable predictions on the decade or century scale are urgently needed today, but temporal resolution in the pre-Pleistocene fossil record is at least two to three orders of magnitude coarser, due to problems such as gaps in the record and vertical mixing of successive populations (*42*). Thus, even truly instantaneous events cannot be distinguished from processes encompassing 10^5 to 10^6 years, particularly on a global scale. Moreover, high-resolution data suggest some measurable duration for most, if not all, major extinctions. Even the end-Cretaceous event, the one most likely to have been triggered suddenly by bolide impact or other environmental shock, apparently involved at least 10^4 to 10^5 years of oceanographic and atmospheric turmoil when analyzed at single sites (an approach that sacrifices global generality for refined local resolution) (*43*). The best-dated extinction of the geologic record, the terminal Pleistocene extinction of large mammals, is currently estimated as spanning about 9,000 years (with onset about 18,000 years ago) (*44, 45*).

The best paleontological extinction data, in terms of geographic coverage and temporal resolution, are for marine invertebrates and microplankton. Most workers consider large databases to be more robust to sampling biases when compiled at the genus level or above, and many argue that the behavior of genera is useful as a damped proxy for species-level processes (*3, 46*). These factors alone would hamper quantitative comparisons to present-day extinctions, but a subtler bias is also at work: the extinctions detected by paleontologists primarily involve taxa that are more widespread and abundant (and thus more likely to be fossilized) than the extreme endemics that constitute some fraction of present-day estimates for endangered tropical species. Many uncommon, localized taxa do enter the fossil record, but species such as those restricted to the now deforested Centinela Ridge, Ecuador [$\leq$20 km^2 (*47*)], would almost certainly fail to be fossilized or collected, and this renders overall comparisons to fossil data problematic. Estimated paleontological background rates are so low [averaging only about 1 to 10% per million years for marine invertebrate species (*48*) but less fully analyzed for terrestrial animals or plants] that tropical extinctions corrected to their potential fossil record would still probably exceed paleontological background rates, but this question requires careful analysis.

One approach to scaling present-day extinction estimates to the fossil record would be to assess how many living species and genera described thus far (which in turn are just a fraction of the 5 million to 30 million living species estimated) actually, or even potentially, have a fossil record. More than 77% of 700 species of shelly marine mollusks of the Californian province occur as Pleistocene fossils (*49*), and comparable proportions probably obtain for vertebrates and plants, particularly for pollen taxa. Given a particular scale of perturbation, then, what is the expected fate of those groups for which the fossil record provides the most robust predictions?

Finally, the disparity of the unknowns in the two systems also hinders detailed use of the fossil record to predict present-day biodiversity losses and their consequences. Paleontologists have a partial record of taxon loss in time and space, and attempt to infer the nature of the disturbances that caused the observed magnitudes and patterns of differential extinction. Linkages between a particular extinction episode and climatic or other potential forcing factors are hypotheses to be tested. In contrast, biologists have partial data on environmental disturbances such as rain forest conversion and attempt to infer or predict magnitudes and patterns of extinction. Again, compiling data on living species that are analogous to paleontological data might be the most efficient means of generating rigorous interdisciplinary extrapolations.

All of these problems are minimized in the youngest part of the fossil record: the last 5.2 million years since the start of the Pliocene, with their oscillations between glaciations and global warming trends, are being explored in increasing stratigraphic, geochemical, and paleobiological detail (*12, 50*). Data on differential survivorship and geographic shifts of late Tertiary vertebrate and plant species in response to increasing aridity and habitat patchiness (*50, 51*) should be useful in inferring potential effects of present-day perturbations. The analogy is imprecise because the late Tertiary changes seem tied ultimately to the onset of global cooling, an unlikely scenario for the immediate future, but faunal and floral dynamics can still be used to good predictive effect given the diversity of present and impending environmental alterations independent of the overall vector of global climate change. Further, the repeated oscillations between glacial and interglacial states that characterize global climates over the past 2 million years provide replicated natural experiments on biotic consequences of rapid shifts in global temperature and rainfall patterns.

The past 50,000 years in particular offer extraordinary opportunities for predicting upcoming biotic changes. Time resolution is on the order of centuries, geochemical tracers permit fine-scale calibration of paleotemperature and other factors, and many of the plant and animal species are still extant, so that past performances can be projected into the future with some confidence. In addition to encompassing the end-Pleistocene extinction of large terrestrial vertebrates (*45*), this interval provides invaluable data on the behavior of species and communities in response to climatic changes, most notably the most recent post-glacial global warming trend. The most important message of this still underexploited record is that ecological communities do not respond as units to environmental change. Pollen and skeletal data show that species are highly individualistic in their behavior, so that few, if any, modern terrestrial communities existed in their present form 10,000 years ago. Instead, they originated in piecemeal fashion by means of shifts in abundance or geographic range of their constituent species and will presumably continue to change composition in response to anthropogenic or natural climatic changes.

The individualistic behavior of terrestrial species in response to Pleistocene and Holocene climate changes is evidently a general phenomenon, known for plants in eastern and western North America (*52, 53*), Europe (*54*), South America (*55*), Australia (*56*), and Africa (*57*), North American vertebrates (*58*), and invertebrates (*59*). This fundamental paleontological insight cannot be ignored in designing nature reserves (*60*): reserves must be sufficiently large and environmentally complex to accommodate the array of disparate geographic range shifts that any climatic change will evoke from the resident species assemblage. Any other attempts to anticipate species behavior—cultivars or pest species, for example—must take these discoveries into account as well.

Late Pleistocene–Holocene extinctions are still controversial, but most authors now assign humans at least an accessory role for the end-Pleistocene megafaunal extinctions (*61*). The Holocene fossil or archeological record has also revealed significant extinction due primarily or exclusively to pre-European human disturbance, particularly in island biotas [for example, more than 50% of the avifauna in Hawaii and other Polynesian islands (*62*), and 49% of West Indies land mammals (*63*)]. These data force a substantial upward revision of estimated post-Pleistocene human impacts and offer rich possibilities for testing hypotheses on causes and consequences of special loss. They also undermine attempts to predict biotic responses to habitat reduction or fragmentation, which are commonly based on species-area relations in modern island biotas that are assumed to be at evolutionary equilibrium. In any case, the fossil data on individualistic species behaviors support arguments that habitat diversity is more important than area per se in refuge design (*60, 64*).

The lessons of the past are inevitably blurry and at a coarse scale. At the present state of knowledge, the fossil record is more revealing of potential long-term consequences than of immediate solutions. However, the history of life on Earth provides an array of worst-case scenarios—including even the mildest of the extinction events in Table 1—that are sufficiently spectacular to militate against inaction. Coordinated research on fossil and extant biotas should yield very real benefits for understanding, anticipating, and perhaps managing the biological changes driven by human activities.

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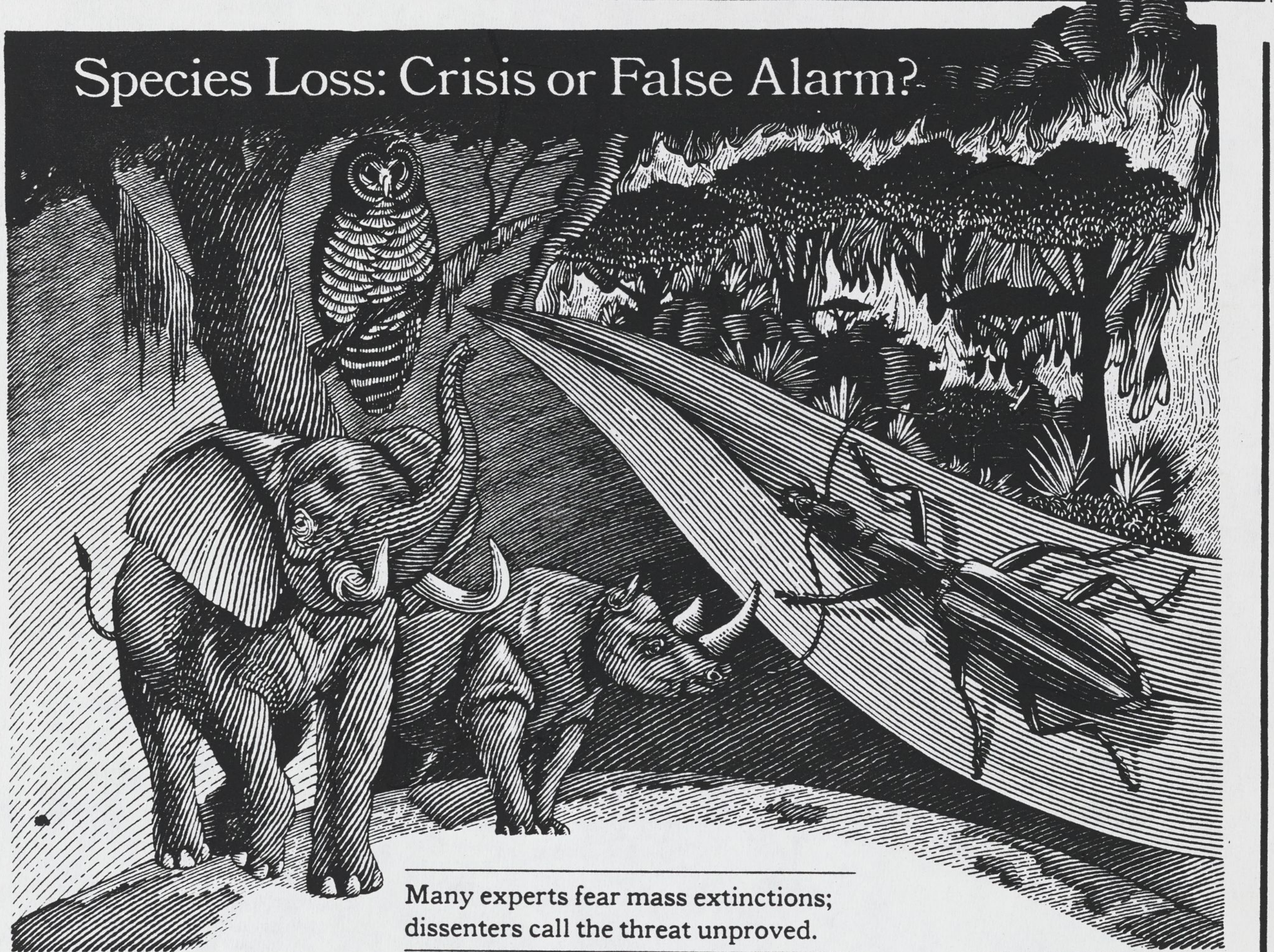
Science Times

TUESDAY, AUGUST 20, 1991

The New York Times

C1

Species Loss: Crisis or False Alarm?



Many experts fear mass extinctions; dissenters call the threat unproved.

The New York Times; Illustration by Brian Callanan

WILLIAM K. STEVENS

RATS, weeds, cockroaches and other hardy, ubiquitous "tramp" species may never inherit the earth. But some scientists say they could make a run for global ascendancy if humans, as many biologists fear, precipitate a mass annihilation of less adaptable creatures.

In this scenario, the actions of an exploding human population are sundering the ecological webs that support life by setting off a worldwide wave of extinctions comparable to the one in which the dinosaurs perished some 65 million years ago.

But is the scenario accurate? A minority of dissenters says that while wild habitats are indeed disappearing because of human expansion, and species with them, the supposed magnitude and rate of the extinctions are unsubstantiated by hard evidence and have probably been exaggerated. In possibly overstating the risk, some critics say, conservationists may harm their own cause by setting themselves up for the charge of crying wolf.

The perceived threat to species diversity has prompted delegates from around the world to meet under United Nations auspices in Nairobi, Kenya, next month in the second of three negotiating conferences aimed at producing a treaty by next June.

Meanwhile, the argument over the seriousness of the threat has surfaced in the current issue of the journal Science. In one of six articles on biological diversity and extinction of species, two prominent biologists, Dr. Edward O. Wilson of Harvard University and Dr. Paul R. Ehrlich of Stanford University, assert that if tropical rain forests continue to be cut down at the present rate, a quarter or more of all the species on earth could be exterminated within 50 years. For the first time in geological history, they say, plant species are becoming extinct in large numbers.

The tropics, and most of all the rain forests, are the richest repositories of biological diversity on earth, and the two biologists point out that many tropical species exist only locally and are subject to immediate extinction with the clearing of a single tract. They say that while conservation efforts are needed, the only way to head off the crisis in the long run is to reduce the scale of human activities.

Since the Science article was prepared, Dr. Wilson said in an interview, he has further estimated that 50,000 species a year, or about six every hour, are being doomed to eventual extinction. The estimates are based on a mathematical model of the observed relationship between habitat area and number of species and on the observed disappearance of rain forests.

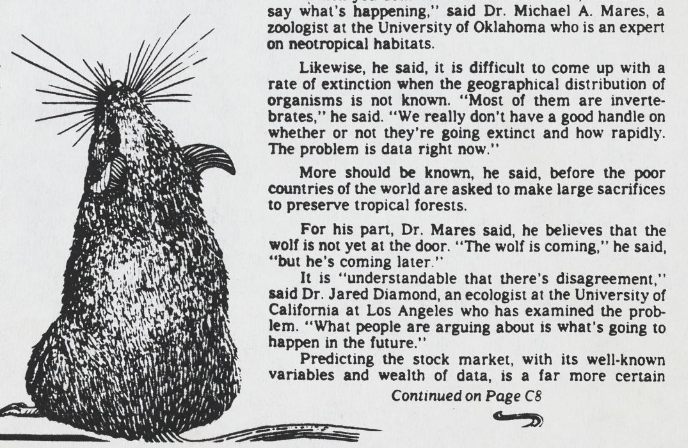
Coral reefs, dry tropical forests and other tropical habitats are also being destroyed. The resulting mass extinction, Dr. Wilson said, is likely to compare with the largest extinctions in geological history and to take place in a much shorter time: decades, perhaps, instead of centuries or millennia. "It is a genuine holocaust," he said.

"That sounds alarmist," Dr. Wilson conceded. "But I invite anyone to check through the figures."

The skeptics have not yet had a chance to examine Dr. Wilson's latest assessments in detail, but they have attacked earlier, similar assessments made by him and other scientists. The critics say there simply is not enough information on which to build a reliable assessment.

Will the Weedy Inherit Earth?

When humans disrupt natural habitats, scientists say, highly adaptable global species like rats and cockroaches invade the disrupted area and replace richly varied assemblies of local organisms. In mass extinctions of the past, fossils show, large vertebrates were more vulnerable than smaller ones.



While species constitute a "valuable endowment" and should be protected, there is "a total lack of evidence" of a biological holocaust, said Dr. Julian Simon, a University of Maryland economist. He is perhaps better known for arguing that the world's resources, coupled with human ingenuity, can support a surging population. "We're being asked to take the entire scenario on faith" and on the judgment of those who advance it, he said. The warnings of mass extinction, he said, "seem like guesswork and hysteria."

Other dissenters say there is a problem, but that its dimensions simply cannot be known at the moment. No one even knows the true number of species in the world, they say. This is acknowledged by Dr. Wilson and others who share his view.

Only 1.4 million species have been identified worldwide, but estimates of South American species alone range from 5 million to 50 million, and estimates of global species range up to 100 million.

"When you deal with that kind of error, it's hard to say what's happening," said Dr. Michael A. Mares, a zoologist at the University of Oklahoma who is an expert on neotropical habitats.

Likewise, he said, it is difficult to come up with a rate of extinction when the geographical distribution of organisms is not known. "Most of them are invertebrates," he said. "We really don't have a good handle on whether or not they're going extinct and how rapidly. The problem is data right now."

More should be known, he said, before the poor countries of the world are asked to make large sacrifices to preserve tropical forests.

For his part, Dr. Mares said, he believes that the wolf is not yet at the door. "The wolf is coming," he said, "but he's coming later."

It is "understandable that there's disagreement," said Dr. Jared Diamond, an ecologist at the University of California at Los Angeles who has examined the problem. "What people are arguing about is what's going to happen in the future."

Predicting the stock market, with its well-known variables and wealth of data, is a far more certain

Continued on Page C8

Loss of Species: A Crisis or a False

Continued From Page C1

pursuit than predicting the future of species, he said.

Dr. Diamond has concluded that, even taking into account all the uncertainties, "something like half the species that now exist will go extinct or will be on the verge of going extinct in the next century" if current trends continue.

Geological history is filled with mass extinctions. The most famous is the wave of extinctions in which the dinosaurs vanished 65 million years ago. Three-quarters of the species on earth were wiped out in that event, paleontologists say.

Extinctions of similar scope took place about 208 million, 367 million and 439 million years ago. An estimated 96 percent of all species disappeared in a mass extinction 245 million years ago in the most extensive wipeout of species in the geological record. Most recently, an estimated 35 percent of species disappeared in an extinction 35 million years ago.

Dispute Over Causes

Scientists argue about the causes of such events. Species become extinct in the natural course of evolution, but this "background" rate of extinction is very low, said Dr. David Jablonski, a paleontologist at the University of Chicago. Some scientists have tried to assign a single cause, like an impact of a meteorite or comet, to the mass extinctions. Others say changes in climate, sea level, ocean currents or ocean oxygen content could do it. In any case, some great environmental disruption, or combination of disruptions, is believed to be responsible in each case.

Writing in the current issue of Science, Dr. Jablonski says that according to fossil studies, widespread species are more likely to survive a mass extinction, whereas specialized species adapted to a smaller area are especially vulnerable. This, he wrote, suggests that disruption and fragmentation of habitat caused by humans are likely to result in the increasing appearance of "widespread, weedy species — rats, ragweed and cockroaches." The weedy species, he said in an interview, "are biologically prepared to cope" with environmental change and are "capable of using a lot of different kinds of resources," like disturbed roadside habitats and human waste.

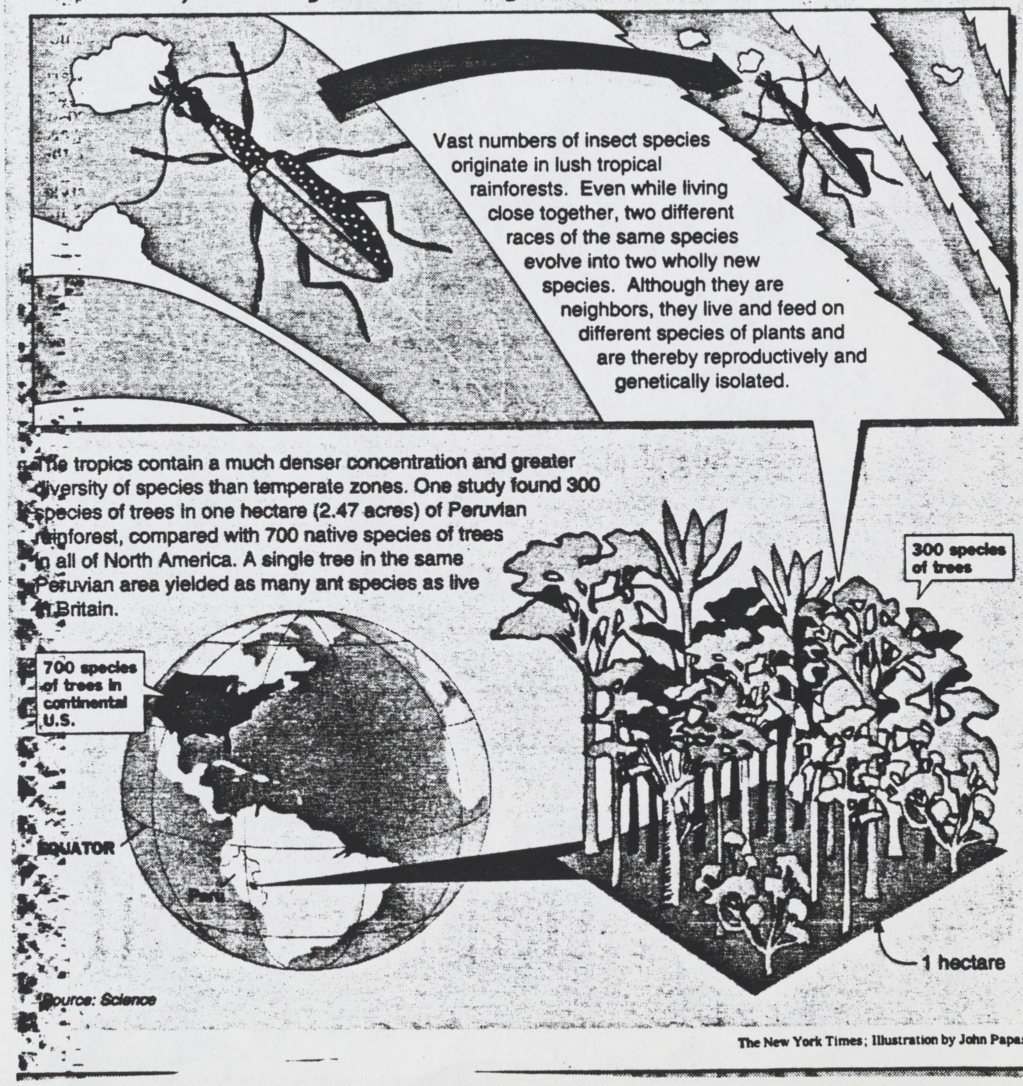
Coming at it from a different perspective, Dr. Terry L. Erwin, an entomologist at the National Museum of Natural History in Washington, wrote in Science that if the disruption of ecosystems continues, "we can expect the evolutionary process as we know it to become degraded and retarded." If current trends continue and are pushed to their extreme, he wrote, "within a few hundred years this planet will have little more than lineages of domestic weeds, flies, cockroaches and starlings evolving to fill a converted and mostly desertified environment."

Specialized species that adapt to specific areas are especially vulnerable.

The big question is whether the disruptions caused by human activity will be enough to create this bleak landscape and to bring about a mega-extinction like those of the distant past.

"That's the $10,000 question," said Dr. Jablonski. "We have no idea how many species are out there and how many are dying. My own personal

Evolution, Density and Variety



The New York Times; Illustration by John Papasian

Alarm?

feeling is that if the destruction goes unchecked, we will reach an extinction level unmatched since the end of the Cretaceous" period, when the extinction of the dinosaurs took place. "Under any circumstance, we're going to have a big loss," he said.

Dr. Simon has argued since the mid-1980's that there is no evidence of extinction rates of the magnitude advanced by Dr. Wilson and others. In an article in 1986, to which he says he still holds, he wrote that "there is no prima facie case for any expensive policy of safeguarding species without more extensive analysis than has so far been done." He says that the only scientifically observed extinction rate in this century is one species a year.

'Massive and Worldwide'

On the contrary, says Dr. Wilson, "the observed extinctions of species in this century have been massive and worldwide." While "our very incomplete knowledge" makes it difficult to monitor extinctions, he said, "in the small minority of groups of plants and animals that are well known, extinction has been found to be proceeding at a rate hundreds or thousands of times above pre-human levels. That has been spread prominently on the scientific and public record."

While no comprehensive global survey has been taken, he says, there are hundreds of separate examples of serious recent extinctions: for instance, 90 plant species whose only habitat was a single mountain ridge in Ecuador, and half the 280 freshwater fish species in peninsular Malaysia.

Dr. Wilson bases much of his case on calculations employing a mathematical model that describes the effect on the number of species when the geographical area in which they exist is reduced. The model, which he says has been tested for validity against field studies and observations "over and over again," calculates that when species' habitat in a given area, an island or a continent, and the habitat is reduced by 90 percent, the number of species eventually declines by about half.

Worldwide, he said, tropical rain forests are being lost at the rate of nearly 55,000 square miles a year, a loss roughly equivalent to the land area of Florida. This figure, he said, was derived recently from satellite reconnaissance and from surveys by governments and scientific teams.

At that rate, Dr. Wilson calculated, the world's rain forests would be reduced by half in 30 years. Applying the area-species model to this finding, he calculated that 10 percent to 22 percent of the rain forest species would be "doomed" in the next three decades.

As used by ecologists, doomed means that extinction might take some time, but that it is a foregone conclusion. Although they cannot be sure, scientists believe that more than half the world's species, from bacteria to big mammals and trees, live in the rain forests.

Criticism on Data

The mathematical model used by Dr. Wilson "is based on nothing but speculation," said Dr. Simon. "If scientific models are to have any validity, they must be based on some solid data." He said he has been unable to find such data.

Critics also say that deforestation statistics can be misleading, that in the Amazon, for instance, more than a third of the region that is considered tropical forest is not rain forest but savanna and semi-desert. They say also that some of the forest is not virgin forest, which is richest in species, but secondary growth. In reply, Dr. Wilson says that his calculations involve rain forest only, and apply globally, and that secondary forest is included as well.

To observations that not enough is known about the number of species in the world, Dr. Wilson says that this is "completely true," but that it makes no difference: Whatever the number, it is the proportion by which the species total is reduced that is important, and this is calculable.

Dr. Mares notes that there was no widespread extinction of species in the eastern United States after its forests were cleared. "While there were quite a number of changes in distribution patterns of many species," he said, "we haven't had massive die-offs."

Dr. Wilson said that in the temperate zones, species tend to be distributed over a wider area than in the tropics, where it is common for a given species to be confined to one mountainside or one river basin. Temperate-zone species, he said, are consequently better able to survive habitat destruction.

Dr. Mares acknowledged this, but said that "when you look at mammals" in the tropics, in which he specializes, "I don't think this is the case. Many have extensive distributions."

Puerto Rico's Experience

Some dissenters have also said that the experience of Puerto Rico casts doubt on the doomsday scenario. There, they say, there are as many species now, or more, than before the arrival of Columbus. Yet the island was largely deforested at the turn of the century.

"That's probably true," said Dr. Wilson, "but it has been loaded up with tramp species, cockroaches, weeds and so forth. Everywhere you go, you get them, and they're the same ones you get in Caracas and Lagos and Miami." Meanwhile, he said, some of the local species have been lost, and those are "gone from the global roster."

That, he said, is the direction in which the world is going, "as we wipe out very rich assemblages of local, endemic species that have taken millions of years to build up, in many cases wiping them out before we have put scientific names on them."

Associated Press

Dr. Edward O. Wilson
Harvard University
"In the small minority of groups of plants and animals that are well known, extinction has been found to be proceeding at a rate of hundreds or thousands of times above pre-human levels. That has been spread prominently on the scientific and public record."

Dr. Julian Simon
The University of Maryland
"There is no prima facie case for any expensive policy of safeguarding species without more extensive analysis than has so far been done."

THE DOOMSDAY MYTHS

By exaggerating environmental dangers, activists have undermined their credibility–and triggered an anti-environment backlash

It used to be that only religious cranks could predict the end of the world with a straight face. No more. Eminent scientific forecasts of imminent global ecodeath have become a routine part of the debate over environmental protection. A petition signed by 1,575 leading scientists says that man's activities may render Earth "unable to sustain life." Vice President Al Gore, in announcing the Clinton administration's environmental initiatives, regularly invokes an equally apocalyptic vision of the future: mass extinctions, cataclysmic climate upheavals, gaping ozone holes. "We have no right to cavalierly risk the ecological balance of this Earth," Gore said recently in an interview with *U.S. News.*

voters informed to level crisis sports

see 90-91

But such warnings of impending doom are now coming under furious counterattack. Recent months have brought a spate of books and articles, most written by conservative academics and columnists, that dismiss all warnings of environmental doom as hoaxes. Columnist George Will has derided Gore's concern for the planet as a government power grab; conservative talk-show host Rush Limbaugh has called global warming a "scam" invented by environmental scientists to increase their research funding, and books with titles like *Apocalypse Not, Trashing the Planet* and *Environmental Overkill* have joined the fray, purporting to debunk as pseudoscience and "scaremongering" everything from acid rain to air pollution and toxic waste.

regulations taxing conspiracy

Coming at a time when Americans are preoccupied with foreign competition, jobs and the deficit, the backlash is having an effect. Although Gore characterizes skepticism on global warming as "unethical" and based upon "kooky theories," industry opposition to tough global-warming measures played a key role in the administration's recently announced compromise plan, which relies almost entirely on voluntary action. Industry has succeeded in getting the administration to compromise on other important environmental issues: The White House earlier this year dropped plans to increase fuel-economy standards for automobiles and allowed logging to continue in 25 percent of old-growth forests—decisions that have outraged environmentalists.

What's driving the backlash? Certainly, none of the global environmental issues now under attack is a hoax. Nor is the political agenda of many of the anti-environmentalists very hard to find. But some environmental researchers now concede that at least part of the blame lies with themselves: Environmentalists' penchant for doomsaying is coming back to haunt them. By overstating evidence, by presenting hypotheses as certainties and predictions as facts to create a sense of urgency, scientist-activists have jeopardized their own credibility. "The front lash," acknowledges Stephen Schneider, a leading climate modeler with the National Center for Atmospheric Research in Colorado, "was a little political, too."

Others, while denying that environmental scientists have deliberately played politics with their data, concede that the distinction between science and advocacy has become blurred as scientists are increasingly called on to make policy recommendations—which often

PHOTOGRAPH BY KEN & CARL FISCHER

baby doesn't get thrown out with it.

means playing down scientific uncertainties. "It's one thing to discuss these things with scientific colleagues; it's another to sit before a panel of policy makers and say this is what we ought to do," says Tom Lovejoy of the Smithsonian Institution, who has advocated urgent action to protect tropical biodiversity. "When you live in a sound-bite world, they don't stand still if you wobble around."

A review of the scientific literature and interviews with researchers suggest that while none of the threats to the global environment can be dismissed, many oft-cited "facts" used to paint a picture of impending ecological disaster are more myth than reality. Only by confronting these myths, some researchers now say, can environmental scientists hope to retain their credibility in the face of mounting skepticism—and get on with addressing the real environmental challenges the world faces. Keeping the water clean, in other

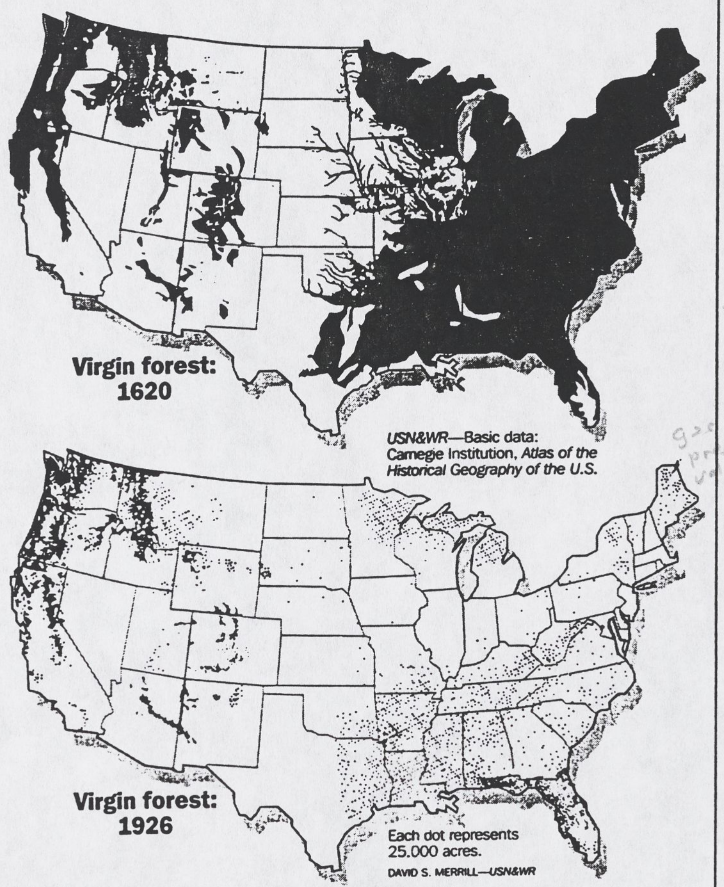
Mass extinction?

Widely quoted predictions of mass extinction are based on a simple mathematical formula that equates a 90 percent loss of habitat with the extinction of half of all species. But when the forests of what is now the eastern part of the United States were stripped to 1 to 2 percent of their original area, only three forest birds became extinct.

Passenger pigeon

Ivory-billed woodpecker

Carolina parakeet



MYTH ONE

Fifty thousand species a year are being lost to extinction

Concern about the fate of endangered species goes back a century or more. But the issue took on a very different character in the late 1970s, when biologists began to warn that what was at stake was not merely this bird or that tiger but the fate of the entire planet.

Although field studies had documented an extinction rate of only one species per year worldwide, in 1979 biologist Norman Myers predicted that the rate would balloon, with the loss of 1 million species by the end of the century. Myers offered no basis for his prediction other than to call it a "reasonable working figure." Nonetheless, the number received much attention and is still frequently cited by activists.

his claim that 4,000, or 30,000, or 50,000 species a year—he has used all three numbers at different times—are being driven to extinction. Such numbers, carrying the ring of scientific authority, have featured prominently in calls to action from environmental groups, and they played a persuasive part in the debate over the U.S. position on recent international treaties to slow deforestation and protect biodiversity.

Wilson cites as the basis of his prediction a mathematical equation known as the species-area curve that relates the size of an island to the number of species found on it. An island 10 square miles in area, for example, is typically found to have half as many species as a similar island of 100 square miles. Wilson argues that tropical forests obey exactly the same rule as their size is reduced. By plugging into the formula the rate at which tropical forests are being cut down throughout the world—Wilson puts it at 2 percent per year—he obtains the figure of 50,000 species lost each year.

The numbers game. Although Wilson says the species-area curve has been "established by hundreds of independent studies," the scientific literature is replete with criticism of the whole concept. Unlike scientific equations that reflect precise, immutable laws of nature—for example, the rule that force equals mass times acceleration—the species-area formula is what scientists call an empirical equation, a mathematical attempt to extract a general rule from a large body of scattered experimental data.

Because it is such a sweeping generalization, the formula may or may not fit a specific case. Many factors besides area determine how many species a habitat can support: climate, terrain, the habits of the species in question. A recent scientific review found that differences in area explain only half the variation in species abundance from one island to another.

Moreover, what may be true for an island is by no means true for a huge area such as a mainland forest. In the eastern United States, for example, during the first 300 years of European settlement, woodlands were broken up into fragments, none larger than 1 to 2 percent of the original vast forest, but only three forest birds became extinct—the carolina parakeet, the passenger pigeon and the ivory-billed woodpecker. Moreover, habitat loss probably did not play the major role in their demise: The parakeet and the pigeon were hunted to death.

Similarly, the Atlantic coastal forests of Brazil have been cut to about 12 percent of their original size, yet a team of

Ragged edge. *Development in Brazilian rain forests maximizes the "edge effect" (diagram, Page 87)—and the ecological impact.*

Brazilian zoologists that combed the forests recently could not confirm a single case of extinction. Instead, they rediscovered several birds and six species of butterfly considered extinct 20 years ago. And a survey by the Flora Meso-Americana project found *increased* abundance of some species considered threatened. "Despite extensive inquiries, we have been unable to obtain conclusive evidence to support the suggestion that massive extinctions have taken place in recent times," writes Vernon Heywood, a former chief scientist of the International Union for the Conservation of Nature and Natural Resources, which works with governments to protect endangered species and habitats.

Natural resilience. Biologists offer several explanations for such "unreasonable" tenacity of species. Many tropical species are widely dispersed, so the loss of one chunk of a forest does not doom them to extinction. Moreover, ecosystems like the Brazilian Atlantic forests may be naturally resilient, having evolved mechanisms to cope with the severe natural upheavals that are endemic to a mountainous climate subject to heavy rains and sudden cold spells.

But most important, says Heywood, "biodiversity is not equally distributed throughout the world." By protecting specific, critical habitats within forests, he says, "a small amount of conservation can skew the curve." He cites a study of African birds which indicates that 95 percent of species are found within areas already protected: three quarters of southern Africa's native plants are found in reserves as well.

K. S. BROWN – UNICAMP

Not extinct. *Recently rediscovered himeros swallowtail butterfly*

While sweeping generalizations about impending extinction catastrophes may get attention, they don't do much to help a conservation planner figure out where to focus his efforts. Worse, they tend to discredit the work of scientists pushing for practical conservation measures that virtually all researchers agree are needed to protect the species that are threatened by a loss of habitat.

Yet the political climate has made it difficult for scientists to challenge the more politically correct views of Wilson. "People are a lot more skeptical in private," says Heywood. "They are very cautious about express-

[publicly], because they don't want to be seen rocking the boat. This is the fear it might damage 'the cause.' " Yet, as Heywood notes, the real damage may come from questionable claims that undermine the credibility of all conservation biology.

MYTH TWO

Forty million acres of tropical rain forest are destroyed each year

Sharing top billing with mass extinction as the environmental *cause célèbre* of the decade is the destruction of tropical rain forests. Images of bulldozers and vast piles of burning timber merge with frightening statistics: as many as 40 million acres a year destroyed, a football field every second.

This figure, like the extinction rate derived from it, has taken on a life of its own, being cited and recited without reference to its origins. Yet almost half the estimated total comes from a very rough estimate made by a Brazilian scientist who used sensors on a U.S. weather satellite to count the number of fires burning in the Amazon at one time in 1988. He estimated the size of each, guessed that 40 percent were burning in recently cleared forest and then multiplied. The resulting number was incorporated into a widely cited 1990 report by the private, Washington, D.C.-based World Resources Institute that helped to fuel the alarm over vanishing tropical forests; this report was cited by Gore and other administration officials last spring in announcing their support for the Biodiversity Treaty and other initiatives to protect the global environment.

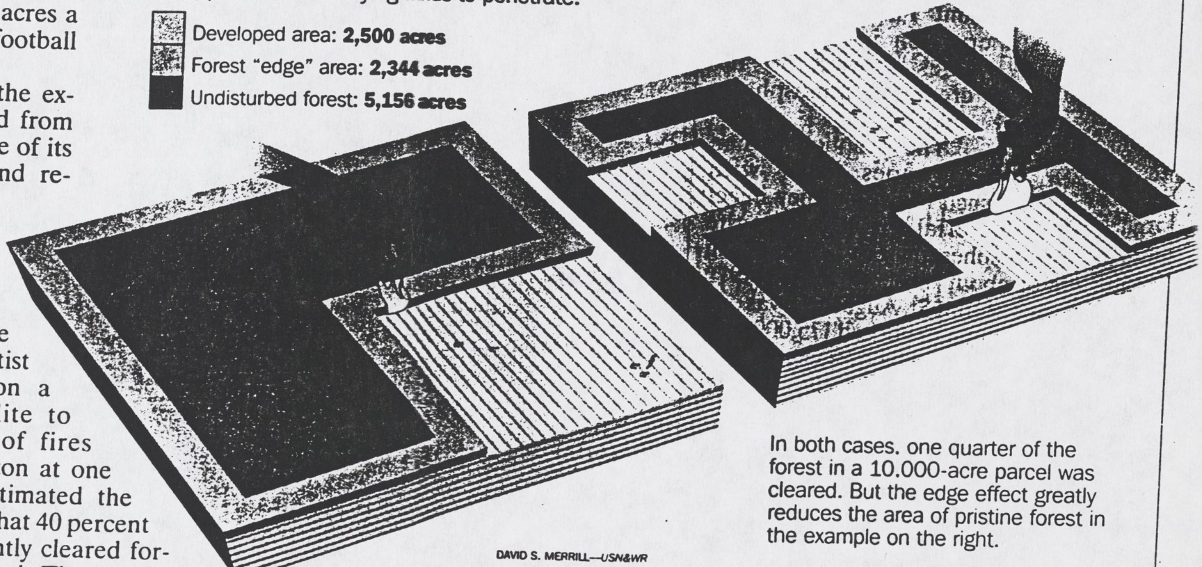
Last summer, two American researchers took a more careful look. Armed with 210 overhead photographs of the Amazon region taken by Landsat satellites, they compared images from 1978 and 1988, painstakingly entering into a computer every tiny forest clearing, road and power-line right of way. They found that the average rate of rain forest loss was 3.7 million acres per year, or about one fifth the widely accepted number.

Conservative commentators seized on the findings to argue that the rain forest issue is a hoax. "There has been, unfortunately, a considerable muddying of the waters by those who have a political agenda," complains David Skole, an ecologist at the University of New Hampshire, who carried out the research with Compton Tucker of the National Aeronautics and Space Administration.

Skole points to a more significant insight from his research that is being lost in the political jousting: The *pattern* of forest clearing matters as much as or more than the total number of acres felled. The main reason is what biologists term the "edge effect." Winds, sunlight and temperature are all altered along a forest border, and their effect penetrates some distance into the forest. Every additional bit of exposed edge also gives cattle, hunters and predators easier access to a forest.

The edge effect

Many small clearings cut in a forest will have a much more drastic impact than one large clearing of the same size: Each exposed forest edge allows predators, poachers and drying winds to penetrate.



In both cases, one quarter of the forest in a 10,000-acre parcel was cleared. But the edge effect greatly reduces the area of pristine forest in the example on the right.

DAVID S. MERRILL—*USN&WR*

On the edge. Dividing a forest into many small patches may leave the total acreage almost the same, but it drastically increases the area subject to the edge effect. One study in temperate forests showed how losses of forest birds to edge-dwelling predators such as raccoons mount dramatically when forests are carved up. Researchers put quail eggs in artificial nests; in a forest of half a million acres only 2 percent of the nests were preyed upon in a week, vs. 70 percent in 10-to-30-acre suburban wood lots.

When Skole and Tucker analyzed the deforestation patterns in the Amazon, they found that even though the total area cleared was about one fifth the previous estimate, the area *affected* by clearing, assuming that the edge effect penetrated 1,000 yards into the forest, was three times the amount lost directly to chain saws. "The areas that are opening up, particularly in the state of Rondonia, where the Brazilian government has an organized development program, are fish-bone patterns" in which a network of roads and farms is laid out every couple of miles, Skole says—a pattern that maximizes the edge effect.

The downward revision of the total deforestation rate undercuts the argument that the issue is a crisis that demands immediate and drastic action such as sweeping curbs on development. But the new edge-effect analysis also suggests that more attention should be paid to *how* forest land is developed.

MYTH THREE

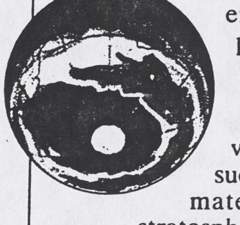
The ozone hole is spreading

After two decades of probing the atmosphere with a welter of instruments carried on spacecraft, weather balloons and highflying U-2 aircraft, researchers thought the case was closed: Man-made chemicals known as chlorofluorocarbons drift into the stratosphere, break down and release chlorine molecules, which in turn attack the ozone molecules that naturally shield Earth from cancer-causing ultraviolet radiation.

Now, a furious counterattack has caught many researchers by surprise. Former Atomic Energy Commission

Chairman Dixy Lee Ray, in her book *Trashing the Planet,* claims that any ozone depletion that has occurred is completely natural, the result of volcanic eruptions and sea spray, not man-made chemicals.

Unnatural reactions. Most of these counterarguments are easily dismissed. Measurements in the atmosphere confirm what basic chemistry suggested all along: Chlorine from most natural sources never reaches the stratosphere. Natural chlorine-bearing chemicals, such as hydrochloric acid from volcanoes and sodium chloride from sea spray, are soluble in water and are washed out of the air by rain. Measurements taken after the 1991 Mount Pinatubo volcanic eruption in the Philippines showed no increase of atmospheric chlorine.



The exception is when volcanoes erupt with such force that they inject material directly into the stratosphere, which begins at an altitude of about 60,000 feet. The 1976 eruption of Mount St. Augustine was one such exception; it deposited 175,000 tons of chlorine, but that is still much less than the 750,000 tons released each year from man-made chemicals.

The only natural source of chlorine that routinely survives the journey to the stratosphere is methyl chloride, which is given off by ocean plankton; measurements show it accounts for only one sixth of the chlorine in the stratosphere. All the rest comes from man-made CFCs, and stratospheric chlorine has been increasing steadily since the 1950s, from 0.6 parts per billion to 3.8 ppb now.

But if Ray and others have exaggerated how much chlorine enters the stratosphere from natural sources, environmental activists have overstated the proven consequences of man-made CFCs. A number of ill-substantiated claims of increases of skin cancer and epidemics of blindness in sheep in South America have received much attention. So did a January 1992 announcement by NASA researchers of a record high measurement of ozone-eating chlorine molecules made by a U-2 aircraft over Bangor, Maine. The data were correct—but subsequent interpretations of them were not. Then Senator Gore chided George Bush for ignoring an "ozone hole over Kennebunkport," where the former president has a vacation home. The findings were also cited

Each winter, extreme cold in the Antarctic triggers a chemical reaction that intensifies the ozone-eating effect of chlorine, punching a hole in the ozone layer (left). But Arctic winter temperatures are milder, thanks to vast wind patterns stirred by the Northern Hemisphere's more mountainous terrain. That has so far prevented a similar hole from opening up over the part of the world where most people live.

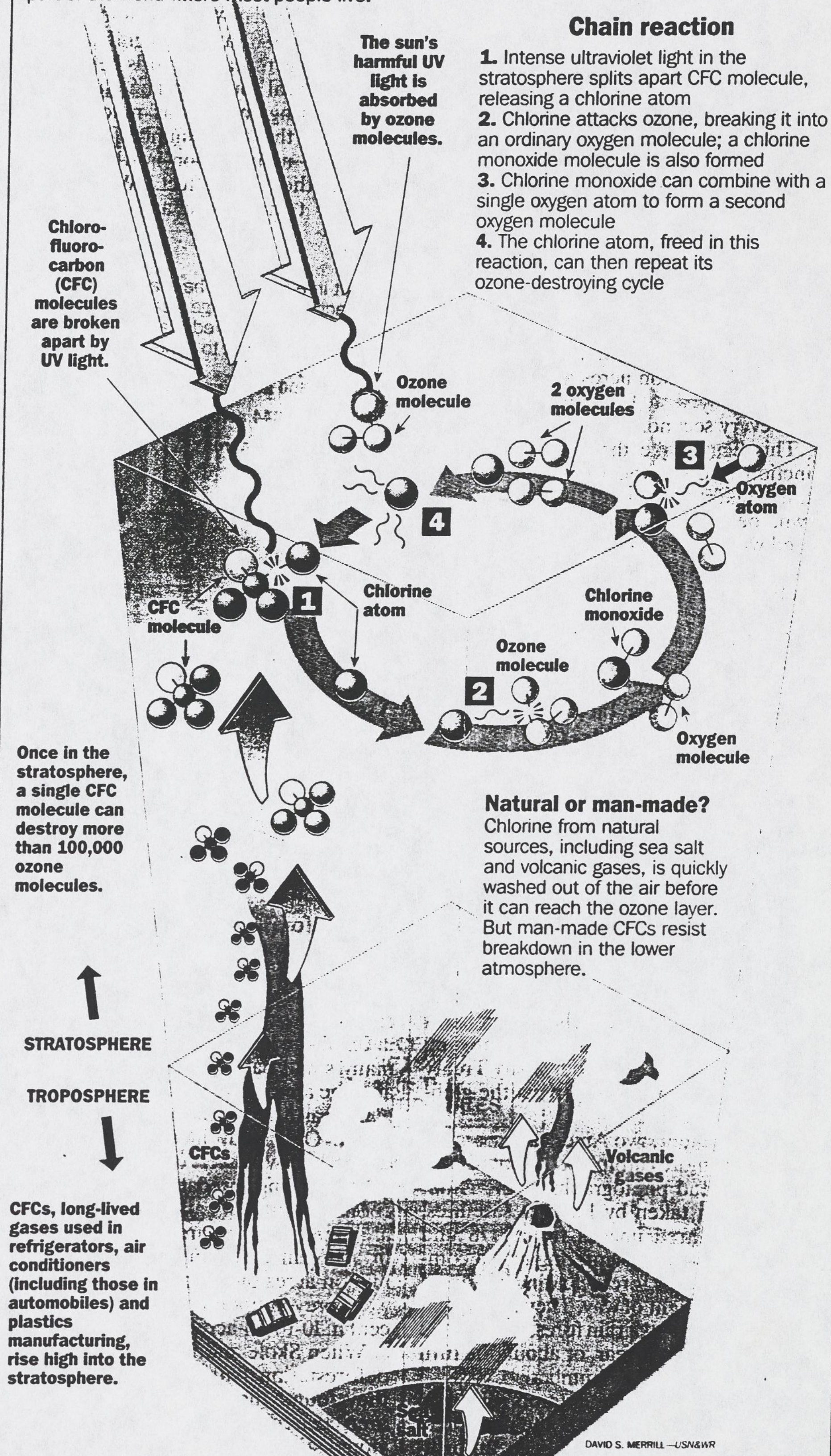


PHOTO: JPL

by advocates urging a speedup of the already agreed-to international phase-out of CFC production.

But the predicted ozone hole in the Northern Hemisphere never materialized, and the NASA researchers, fairly or unfairly, ended up with egg on their faces. The reason was a warming trend in late January 1992. Polar winter temperatures usually accelerate ozone loss: Nitric acid, which in warmer conditions forms an atmospheric gas that binds to some of the chlorine to keep it out of circulation, condenses at -78 degrees Celsius, and chlorine concentrations then shoot up. The January thaw reversed the process, and chlorine levels dropped.

"Poor science." "It's very poor science to assume that ozone is dropping based on circumstantial evidence of increased chlorine," acknowledges Harvard's Jim Anderson, one of the NASA-funded researchers. "People who say we have not established a cause-and-effect link in the Northern Hemisphere are correct." In the Antarctic, measurements taken by Anderson and others have confirmed the connection between elevated chlorine and depleted ozone. Antarctic ozone holes have appeared every spring since the mid-1970s and have been growing deeper each year; up to 80 percent of the ozone disappears over an area equal to 10 percent of the globe's surface.

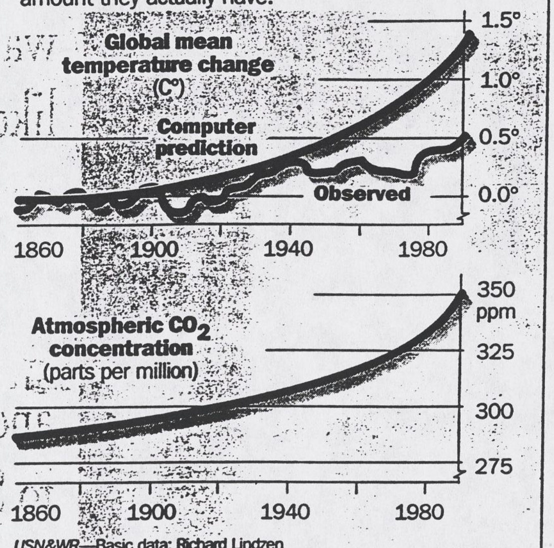
But the Antarctic ozone hole is the product of *two* factors: man-made chlorine and extreme cold. Although man-made chlorine is distributed throughout the stratosphere, extreme cold is confined to polar winters. So the existence of the Antarctic hole does not in itself prove that severe ozone depletion also will occur in more temperate regions.

In fact, some natural processes may counteract the ozone-depleting effects of CFCs at midlatitudes, especially in the Northern Hemisphere—where most of the world's population is concentrated. The large number of mountain ranges in the Northern Hemisphere acts to stir up the atmosphere, pumping heat to the North Pole; the Arctic stratosphere stays about 10 degrees warmer than the Antarctic. That prevents chlorine-binding nitric acid from condensing out of the air. Air currents also work to shuttle ozone from the tropics to the midlatitudes, replacing some of the loss.

DAVID S. MERRILL—USN&WR

Global warming—sort of

If computer models that predict global warming as a result of rising CO_2 concentrations are correct, average temperatures should already have risen by more than twice the amount they actually have.



USN&WR—Basic data: Richard Lindzen

The fact that the stratosphere is higher over the midlatitudes than it is over the poles poses a fundamental problem for researchers trying to make the case for man-made ozone depletion over the temperate zones. Because the stratosphere there lies beyond the reach of U-2 aircraft, direct, simultaneous measurements of ozone and chlorine are difficult. (NASA has proposed buying an unmanned, highflying aircraft to gather the needed data.)

Much depends on the answer. The industrialized nations have agreed to terminate CFC production by 1996, but China, India and Brazil have been given an additional 10 years to comply, and all three will be potentially huge producers as they industrialize over the next decade. It may turn out that the stratosphere can absorb the blow and the damage will remain confined to the Antarctic in winter. But if not, the damage will persist for a very long time: The stratosphere flushes itself out very slowly, and the chlorine already there will persist for hundreds of years.

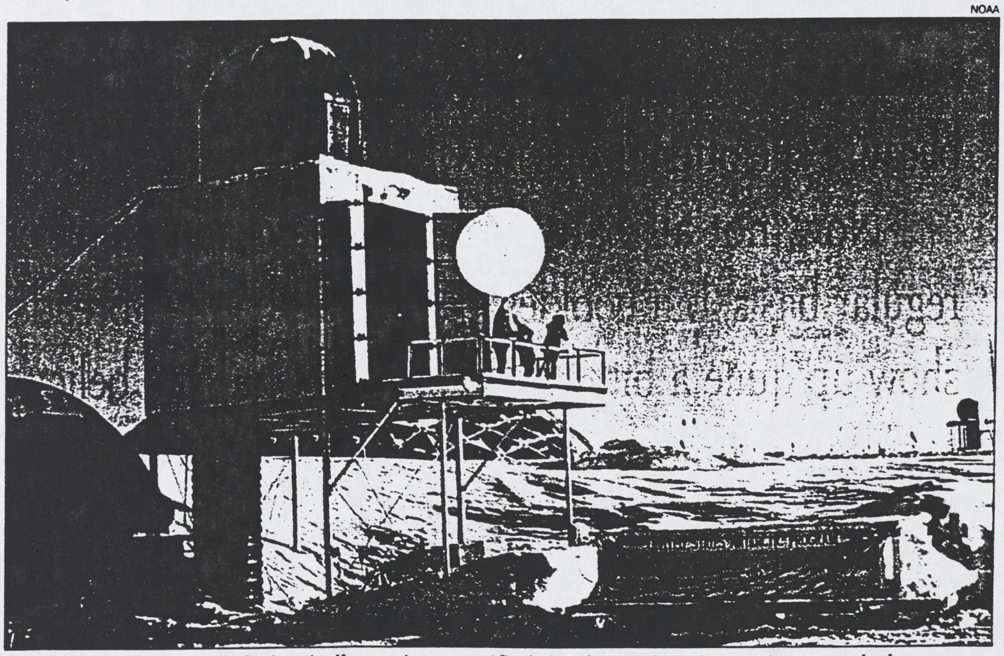
MYTH FOUR

No serious scientists doubt predictions of global warming

To environmentalists, global warming is "a holocaust" or "the end of nature." To the political right, it is a trojan horse for expanded government powers.

The issue started to heat up politically in the 1980s, when Senator Gore began to argue that computer models forecasting

NOAA



Soundings. *Instrument-laden balloons have verified the deepening Antarctic ozone hole.*

a warming of the planet were not merely theoretical predictions; the scientific community, he said, accepted their results as near certainty. Those who still question this, Gore recently told *U.S. News*, are suffering "a massive case of denial" and have "willfully put out false, scientific pseudo facts to pollute the public debate." He added: "Some of the so-called scientists who put out these kooky theories get money from industries that profit greatly from the current pattern ... there are institutes funded by coal companies that have an interest in not seeing any change take place."

Doubters. Yet doubts about the likelihood, intensity and consequences of global warming extend far beyond a few fringe scientists or industry hirelings.

This much is certain: Carbon dioxide, water vapor and several other atmospheric gases trap heat that otherwise would radiate from Earth, leaving the planet to freeze. And since 1750, the concentration of carbon dioxide in the atmosphere has increased from 275 ppm to 355 ppm as the burning of fossil fuels has expanded. (The data come from direct atmospheric measurements since 1958; air trapped in the ice that builds up each year in polar ice sheets has preserved a record of earlier years.)

GEORGE F. MOBLEY - NATIONAL GEOGRAPHIC SOCIETY

Core of the matter. *Digging up ancient climate records*

Beyond such basic facts, however, uncertainty reigns. Computer models of the atmosphere calculate that a doubling of the carbon dioxide concentration, which could occur in the next century if no action is taken to limit emissions, will cause a 1-to-5-degree Celsius rise in average global temperatures.

But there are two major problems with the models. First, the current models account only very roughly for the large role the oceans play in determining the flow of heat in the atmosphere. Second, as physicist Richard Lindzen of the Massachusetts Institute of Technology, a persistent critic, notes, most of the temperature rise calculated by the models comes about not from the increase in carbon dioxide itself but from an increase in the concentration of water vapor in the air, which the models calculate as a secondary consequence of rising temperatures.

Lindzen argues that there is no physical theory or evidence to support the assumption that water vapor increases in the atmosphere as temperature rises. "The only reason to think that is that warm air *can* hold more water vapor," he says. "That's equivalent to saying, 'I have a 2-liter beer mug, you have a 1-liter mug, so mine will always have more beer in it.' " In some models, Lindzen adds, the increase in water vapor is nothing more than a computational glitch that arises because the models crudely slice the atmosphere into only 10 or 20 layers; sometimes, the models even calculate a negative water vapor concentration at some altitudes, then paper over this absurdity by arbitrarily shuffling the water vapor to other altitudes to even things out. Without the assumptions about increasing water vapor as temperatures rise, Lindzen says, no model would predict a rise of more than 1.7 degrees Celsius for a doubling of carbon dioxide; most would calculate no more than 0.1 to 0.2 degrees.

"Can you predict what's going to happen in the next couple of decades with any certainty? I'd say probably not," says Harvard planetary scientist Michael McElroy. "The models are all in one respect or another deficient."

Reality check. That has led both proponents and critics of the global-warming theory to use historical temperature records to try to make their case. Proponents note that average global temperatures have risen in the past century. Skeptics counter that the temperature increase, about 0.5 degrees Celsius, is less than half what the models predict given the carbon dioxide increase to date.

The problem with all such analyses is that *natural* cycles of warming and cooling are always occurring. Since the end of the Ice Age 15,000 years ago, there have been one or two centuries in each millennium in which temperatures have risen half a degree. That means there is a 10 to 20 percent chance that the temperature rise in the past century is part of a natural warming cycle and has nothing to do with carbon dioxide. On the other hand, says climate modeler Stephen Schneider, "there's an equal chance that we're in a natural cooling trend now, and thus our effect is twice as big."

Trying to spot a general warming trend while it's happening is almost impossible, says McElroy: "I really do not believe we're likely to suddenly have someone say, 'Eureka, the greenhouse is here!' If we ever do get to that point, we'd already be in bad shape."

But even some of the strongest skeptics agree that it is sensible to reduce carbon dioxide emissions for reasons that have nothing to do with the greenhouse effect. Fred Singer, a professor of atmospheric chemistry at the University of Virginia and a vocal critic of global-warming predictions, argues that an increase in the gasoline tax, energy conservation and improvements in energy efficiency all make sense under any circumstances. That kind of common sense is much less dramatic than predicting "the end of nature." But it may serve both science and the environment better in the long run. ■

BY STEPHEN BUDIANSKY

Acid 4

Ecological Applications, 2(2), 1992, pp. 124–130

A VIEW OF NAPAP FROM NORTH OF THE BORDER[1,2]

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Abstract. Despite widespread political interference with programs and confusion of science and policy, the NAPAP program has produced a number of sound, if not outstanding, publications documenting the effects of acidic deposition. NAPAP's outstanding strengths in aquatic science are in paleoecology and spatial surveys of chemistry. NAPAP has severe shortcomings in documentation of temporal trends, in deducing biological responses to acidification by organisms other than fish, in considering the effects of nitrogen deposition, and in considering results from countries other than the USA. Summaries of the NAPAP program in 1987 and 1990 underrepresent the extent of damage caused by acidification, as documented elsewhere in NAPAP's publications and by the peer-reviewed literature at large. Overall, it represents a mediocre return for a large amount of investment, and is a poor model for future large, multidisciplinary science projects.

Key words: acid precipitation; acid rain policy; NAPAP.

Introduction

It is premature for me or anyone else to attempt an overall assessment of NAPAP, the National Acid Precipitation Assessment Program. I have only received some of the published State of Science and Technology and Regional Case Study volumes, and haven't had time to read more than a few of them. Many of NAPAP's studies are still not finished. However, I have reviewed many draft manuscripts either directly for the reports or for journals, and have seen a number of recent publications. I have also had periodic contact with many of the aquatic investigators for over a decade. There is some very good science in NAPAP, but not 570 000 000 dollars worth. On the basis of what I have seen, I hesitate to recommend it either as a blueprint for future mega-scale studies, or as a model multidisciplinary study.

NAPAP provides a remarkable case history. It includes political interference with the course of science, obfuscation of scientific conclusions, and delays in the release of first-class science that did not support political agendas. First-class American scientists who would not conform with NAPAP's political objectives were virtually isolated from the program. Yet NAPAP ultimately produced some very good science, and some of the best has now been published in prominent refereed journals and easily accessible books where it is readily available. If nothing else, the history of NAPAP proves that American science is resilient! To put NAPAP in perspective, it is necessary to review parallel American activities with respect to acid precipitation.

[1] Manuscript received 10 October 1991.
[2] For reprints of this Special Feature, see footnote 1, page 103.

Acid Deposition Research before NAPAP

Many of the North American studies now regarded as classics in acid rain research were done before NAPAP or any other formal acid deposition program. The discovery that the problem was present in North America by Gorham and Gordon (1960), the proof that it was a widespread problem by Likens et al. (1972), and the documentation of rapid and devastating effects on fishes by Beamish and Harvey (1972) must be regarded as seminal works. In the late 1970s the NADP (National Acid Deposition Program), a small-budget operation administered by Ellis Cowling from North Carolina State University, was the only sign of an American program to study acid rain. Only a few hundred thousand dollars a year were available, allocated on the basis of peer-reviewed proposals. Funding was available directly to university investigators and even foreign scientists—indeed, NADP actually awarded our group funds for experimental lake acidification in Canada, although the ensuing rapid decline in relations between the United States and Canada over acid precipitation prevented us from ever accepting the money. This was also the era when straightforward negotiations were in progress toward a memorandum of intent (MOI) between Canada and the U.S. to control acid precipitation. The scientific basis for the MOI was provided by a group of knowledgeable scientists from both countries. Remarkably, the major issue at the time was whether Canadian emissions from a small proposed coal-fired power plant at Atikokan, Ontario, would cause significant acidification in the Boundary Waters Canoe area in northern Minnesota! This small initial focus broadened very quickly once the extent of trans boundary movement of strong acids and their precursors in the atmosphere was assessed.

NAPAP, 1980–1987

NAPAP was created to supercede NADP in 1980, just before the Reagan administration's assumption of power in January 1981. Funding was increased manyfold, and administration of funds was transferred from the trusted NADP group to the United States Environmental Protection Agency (EPA), Department of Energy (DOE), and other federal departments. For the next several years, NAPAP cannot be evaluated in isolation from the U.S. political agenda and the actions of powerful federal departments. It became particularly closely linked with policy branches in EPA (then in the notorious Gorsuch era) and DOE. Peculiar things happened. Knowledgeable American scientists on the MOI negotiating team were replaced by virtually unknown junior scientists, most of whom had no previous experience with acidic deposition. Almost all of them were skeptical that acid deposition was a problem. Dialogue over how to decrease acidic precipitation was replaced with the philosophy that "not enough is known." This view fit well with the American Political Agenda at the time, and with the hunger for new funding by U.S. aquatic scientists. Incredibly, the first MOI (1983) had two summaries reaching vastly different conclusions: one Canadian and one American! The American summary largely ignored all previous research on the acid deposition problem, even though some was internationally regarded as of high calibre.

Many U.S. scientists who were internationally known for the excellence of their acid rain work disassociated themselves from the NAPAP program. The lack of guidance from experienced scientists in its early years left NAPAP floundering, and the program appeared to rush off in all directions, sponsoring science that was not really pertinent to assessment of the damage caused by acid rain, or to developing useful emission control policies. The publications and talks on acid precipitation of such notable ecologists as Gene E. Likens, Eville Gorham, Orie L. Loucks, and Gary E. Glass seemed as if they were describing a different country than the one represented by NAPAP. The report of the U.S. National Academy of Science's Committee on the Atmosphere and the Biosphere (CAB 1981), which expressed the opinion that acid precipitation was an important environmental problem, was widely discounted as biased, even though the report was subjected to the Academy's usual stringent review process before publication. The sources of criticism proved impossible to trace, and no specific criticisms of the report's contents were ever committed to paper. For example, statements denigrating the report were attributed by the media to the President of the U.S. National Academy of Sciences and the Chairman of the U.S. President's committee on acid precipitation, even though both individuals denied that they had ever made such remarks! It was even rumored that the report was a "Canadian Conspiracy," due to the inclusion of several well-known Canadian scientists on the committee.

Curiously, the Reagan administration, widely known for its disregard for the environment, indulged NAPAP by allocating more and more money. Many huge acidification projects were begun, eventually involving >3000 scientists and a half-billion dollars. The "not enough is known" slogan was used by agency policy officials as license for both lavish scientific funding and for delaying any controls of sulfur oxide emissions. This stage of NAPAP reached its climax in 1987, when the executive summary of NAPAP's interim assessment (NAPAP 1987) stated that the acid precipitation problem was small and exaggerated—a statement that brought scathing criticism from eminent non-NAPAP scientists both within the U.S. and internationally (for example, see Roberts 1987).

I was among those critical of the 1987 NAPAP report. For brevity, I will give only one example of the many reasons for disagreement with NAPAP's conclusions. One key point of contention in the aquatic ecology part of the 1987 NAPAP report was its assertion that few American lakes were damaged by acid rain because their pH values were not <5. Studies in Scandinavia, Canada, and the U.S. had already shown that biological damage began to occur at pH values <6.0 (Okland and Okland 1980, Eilers et al. 1984, Schindler et al. 1985), but these were ignored by NAPAP's interim report. NAPAP also used absolute pH rather than pH change to assess damage; for example, a lake following the same course as our experimental Lake 223, where pH decreased from 6.5 to 5.05, would be classified as undamaged by NAPAP's criterion, despite evidence from our work that an overall decrease in the number of species of 30–35% would result (Schindler et al. 1985). On the other hand, a bog lake with a natural pH of 5 would be considered as damaged.

Despite the total lack of scientific evidence, NAPAP concluded that rapid reductions in acidifying emissions would have little positive effect on lakes (a conclusion now refuted by studies in Canada, Norway, and Sweden, reviewed by Schindler et al. 1991).

Key pieces of NAPAP research that showed declining pH values in the 20th century (for example, paleoecological studies in the Adirondacks) were mysteriously omitted from the 1987 interim report, even though results had already been widely exposed in international scientific meetings. These shortcomings in NAPAP's report led the Canadian Minister of Environment to refer to it as "voodoo science." NAPAP was regarded by the international scientific community as a laughingstock. A number of key politicians entered the fray, attempting to silence critics of NAPAP with threats of defamation lawsuits, termination of research funding, or, in the case of scientists outside the U.S. like myself, objections through diplomatic channels. Shades of Lysenko and the McCarthy era! (This will be a juicy chapter in my memoirs someday.) This stage of NAPAP terminated with the resignation of NAPAP's director, J. Lawrence Kulp. Shortly thereafter, a NAPAP representative officially retracted the summary volume at a Congressional hearing (Loucks 1992).

NAPAP 1987–1990

Resurrection of scientific credibility became a major objective of the final phase of NAPAP, under James Mahoney. Scientific results were exposed to criticism in international meetings and by solicited peer reviews of regional case histories, state-of-science documents, and journal manuscripts. Scientific criticisms of the program's findings were printed in public review drafts of the document. As a result, the final >6000-page report of NAPAP, and resulting primary publications, are vastly different from the interim assessment. The 20th-century decline in pH of a high proportion of acid-sensitive Adirondack lakes is conclusively deduced from paleoecological evidence, and NAPAP concludes that acidic deposition has caused the acidification of many lakes and streams in the eastern U.S. In the Adirondacks and elsewhere in the Northeast, numerous populations of trout and forage fishes have been lost. Seventy-five percent of acidic streams and 47% of acidic lakes in the eastern U.S. are acidic because of acidic deposition (Baker et al. 1991). NAPAP now agrees with others that lakes begin to become biotically impoverished at pH values below 6.0, an acidity threshold 10-fold lower than that used in the interim assessment. It also concludes that reducing sulfur emissions would cause lakes to recover rather rapidly (though real data from Canada and Scandinavia, where sulfate emissions have now been reduced for 10 yr or more, still indicate that the recovery will be more rapid than that predicted by the unvalidated, expensive NAPAP models). Only key NAPAP officials know whether this turnabout was the result of declining political interference in the post-Reagan era, or more enlightened project management—but in either case Mahoney brought about a major improvement in NAPAP.

Incredibly, the executive summary of NAPAP (called "Draft Assessment Highlights") once again reads like it is summarizing something other than NAPAP's science. Even though NAPAP reports describe a scientific problem of enormous proportions, the executive summary greatly understates the problem. The strong effects of acidic deposition on eastern freshwaters documented in the report and, for example, by Baker et al. (1991) and Sullivan et al. (1990) are not mentioned. Effects of acid deposition on health, soil, and forest problems are made to sound as if NAPAP research has given them a clean bill of health, while the actual reports either show strong correlation with acid rain or that no conclusions can be drawn until further studies are done. As a result, considerable mistrust of NAPAP and its programs remains among scientists, as well as in the environmental community (see, for example, Moore 1991, Loucks 1992). The television program "60 Minutes," where Mahoney and scientists cynical about the severity of the acid precipitation problem soft-pedalled the results of NAPAP and other recent acidification studies, served to heighten the mistrust. Clearly, the "Highlights" agenda is not a scientific one.

NAPAP's Lists of Publications

The huge size of NAPAP's final report makes it very unlikely that any one scientist will ever read it thoughtfully from cover to cover. I certainly don't intend to. There are gold nuggets, but separating them from the pedestrian is analogous to placer mining. NAPAP references also contain an extremely high proportion of "gray literature"—meeting abstracts, intra-agency reports, conference proceedings in publications that are not readily accessible and are not peer reviewed. The list is also padded, at least to a slight degree. For example, I was surprised to find a paper that I co-authored on the list of NAPAP's publications, even though it was not supported by NAPAP and was totally unrelated to any NAPAP objective. Likewise, Gene Likens's book on Mirror Lake is on NAPAP's list, even though it is not really an acid precipitation study, and was never funded by NAPAP (G. E. Likens, *personal communication*). Some papers are also listed in more than one category, making the total list of publications appear larger than it really is.

A perusal of titles and authors, plus what I have read, leads me to believe that the parts of NAPAP dealing with atmospheric transport, chemistry, and paleoecology are quite strong, the agricultural and fish-related parts mediocre, the forest parts weak (largely due to being late in starting), and aquatic biology other than fish and paleoecology are almost non-existent. Modelling efforts, both of water quality and atmospheric transport/transformation are also quite sophisticated, although the scarcity of field studies leaves most of the models unvalidated and curiously devoid of ecological content. It is discouraging that in the total list I could not identify one real "breakthrough" in the understanding of acid deposition, though there are some good, solid pieces of documentation.

The price tags for some of the studies are outrageous. Canadian scientists used to joke that the money used by NAPAP for visual aids in meetings would be enough to fund the entire Canadian acid precipitation program.

Among the problems scarcely touched by NAPAP are: nitrogen emissions and deposition, episodic acidification, ecosystem-scale and long-term studies, and studies of the effects in Canada of American emissions (for example, in Report 9: Current Status of Surface Water Acid-Base Chemistry [NAPAP 1990], Canada merits 34 pages, the world outside North America only 15). Cook (1988) edited an interim report on the acid rain problem in Canada for NAPAP.

Megaprojects and Megamodels: How to Blow $570 000 000

NAPAP represents the ultimate American fixation with scientific megaprojects, megamanagement, and megamodels. Its Regional Acid Deposition Model (RADM) consumed millions of dollars, thousands of man-hours, and years to build. Hourly emissions of pollutants from all major sources, their transport and reactions in the atmosphere, and deposition patterns are combined. Yet one must agree with Roberts (1991) that the model does not go significantly beyond the hazarded guesses of a 1983 National Academy Committee (NAS 1983), that local differences in emissions did not matter when managing a problem on a large regional scale. The RADM model was not completed in time to affect sulfur oxide control policies (in all fairness, it was not designed to be), and it probably would have had little effect on Congress's decision to control sulfur oxides even if it had been available.

Several plans to acidify entire watersheds were afoot in the early 1980s, and several multi-million dollar proposals for such programs were circulated by NAPAP in the ecological community. These proposals revealed an interesting difference between agency funding in the U.S. and Canada. At one point a group of EPA administrators and internationally reknowned ecologists descended on the Experimental Lakes Area to view a watershed-scale acidification project that we had "bootstrapped" on a wetland system. Using a low-head site near a lake, which allowed us to use the research station's garbage tractor to power irrigation pumps, an election-year unemployment reduction program, and some moonlighting by volunteers, our project cost <$50 000 to construct. It has run for 9 yr, for <$100 000 per year. (After 8 yr the recovery phase of this study was begun in 1991.) We had plans to do the same with a nearby forested watershed, but were never able to find the necessary $250 000, despite good scientific reviews. An attempt to obtain NAPAP money for a group of University of Minnesota scientists to participate in these studies, with matching funds provided by Fisheries and Oceans Canada also failed, despite excellent reviews and a proposed budget an order of magnitude lower than proposed for other sites. Politics were, and still are an important part of NAPAP's agenda.

When a NAPAP-sponsored watershed acidification was finally launched in 1988, it had a multimillion dollar price tag. It ran for only a few months before its budget was cancelled, much to the chagrin of the many scientists who spent months designing and planning it.

Millions of NAPAP dollars were also spent on the National Surface Water Survey (NSWS), "snapshot" late-summer chemical fingerprints of lakes and streams done by using helicopters (Linthurst et al. 1986, Landers et al. 1987). These studies yielded a very nice, if expensive, data set for late-summer chemistry, which we (Schindler et al. 1989*a, b*) and others have used to construct models of damage to lakes from acidic deposition. But there is no temporal analog to this massive study. No long-term studies were done in NAPAP, despite its 10-yr lifetime, despite the fact that rates of acidification were one of the key issues in the acid precipitation debates. Even seasonal studies done as a second NSWS study are still to be reported.

Perhaps the best value of large NAPAP aquatic programs was the paleoacidification study. This study was actually begun by the Electric Power Research Institute, in its PIRLA (Paleolimnological Investigation of Recent Lake Acidification) study. Over 20 scientists from a variety of institutions participated. It joined NAPAP mid-stream. Using the dated fossils of pH-sensitive diatoms and chrysophyceans in lake sediments, the PIRLA group showed conclusively that most of the 40% of lakes in the Adirondacks with original pH values <6.0 had acidified in the 20th century. To the disappointment of cynics, the timing of lake acidification verified that acid precipitation rather than land-use changes had caused the declines (Charles et al. 1990). The extent of acidification in other areas of the U.S. was also assessed, and shown to range from moderate to almost nonexistent, depending largely on the acidity of deposition. Many of the participating scientists are now analyzing other environmental problems, such as effects of trace metals and climatic warming. Due to decades of disregard for long-term monitoring and biological surveys, this paleoecological group will have to provide the background information for assessments of change in American ecosystems for decades to come, an example of how NAPAP's total value will only emerge in the decades ahead.

As mentioned above, NAPAP's assessments have been based on data collected in the "lower 48 states" plus a very cursory review of results in Canada and other countries (see also Roberts 1991). The fact that acidified lakes in Canada numbered in the hundreds of thousands, rather than merely thousands (for example, Minns et al. 1990), is unmentioned, but it should certainly be an important consideration in U.S. policy development.

The passage in 1990 by Congress of sulfur oxide emissions controls as amendments to the Clean Air Act has resulted in much criticism, most from proponents of the coal, oil, or power industries, who argue that the environmental benefits will be too few to justify the enormous cost of control technology. I doubt whether this would be the case if Canadian environmental benefits were considered, a shortcoming that NAPAP could still remedy. Optimistically, NAPAP may look better in retrospect. Some of the young scientists who began their careers with NAPAP with little guidance have emerged as mature, respected scientists. Many of NAPAP's most important projects began late or were delayed for bureaucratic reasons, and results will still be forthcoming.

What More Should We Have Expected?

What more could be expected of half a billion dollars? About 10-fold more. Only one ecosystem-scale experiment, the Little Rock Lake Project, was included in NAPAP, despite the internationally recognized need for such studies, and the presence of several internationally famous ecosystem experimentalists in the community of U.S. acid rain scientists. Without frequently applied peer pressure to EPA from the international scientific community, the Little Rock Lake study would have been terminated before it could fulfill its study objectives. Other proposals for ecosystem-scale projects proposed Pentagon-style budgets, bureaucratic and logistic nightmares for project management, and peculiarly intractable hypotheses or study objectives. It is obvious that the talent for designing affordable, tractable ecosystem-scale studies is still the province of a few individuals, not megaproject panels.

I believe that a few well-designed experiments initiated early in NAPAP could have provided conclusive tests of some key hypotheses. A few decade-long studies in areas like the Adirondacks would have yielded valuable information on long-term trends in lake chemistry and biology. Even the deployment of a few biologists with nets to document the presence or absence of acid-sensitive taxa would have allowed some assessment of the extent of biotic impoverishment in lakes and streams. The U.S. still does not have the background biological survey that S. A. Forbes called for over a century ago (Forbes 1883)!

NAPAP's fish results for the Adirondacks underscore the urgency of this undertaking: the disappearance of fishes in the past several decades from all causes was three-fold higher than could be attributed to acid deposition alone. In the case of brook trout, 32% of populations had disappeared in <20 yr. For forage fish a whopping 45% of populations disappeared in the same period! Causes of this biotic impoverishment are not described in detail, but are reported to include reclamation, changes in stocking policy for sport fish, and introductions of exotic species as well as lake acidification. Our modelling results also suggest widespread biotic impoverishment of lakes in the northeastern U.S. (Schindler et al. 1989*a*, *b*).

What Could NAPAP Still Do?

NAPAP will continue for some time, and useful studies could still be undertaken. Damage to Canadian aquatic ecosystems caused by American emissions has still not been addressed. No analyses of the effects of recent control policies on ecosystems in either country have been done. I am sure that inclusion of even a rudimentary analysis of the Canadian situation would stem much of the recent criticism of the amendments to the Clean Air Act by pro-industry lobbyists. Important studies also remain to be undertaken in the U.S. Documenting rates of ecosystem recovery under reduced sulfur oxide emissions is essential for evaluating future policy; this is always better done in hindsight, and its value is almost always overlooked. NAPAP could still undertake a biological survey, which would give a baseline for evaluating recovery of lakes, as well as for biotic impoverishment caused by stresses other than acid rain. The effects of nitrate and ammonium deposition, already recognized as important in Europe, deserve more study (Kelly et al. 1990). Episodic events and nitrogen deposition remain as largely unassessed problems. Studying the recovery of Little Rock Lake would provide valuable insight into how rapidly and completely acidified lakes might recover. One reason that the NAPAP assessment to date still minimizes the effects of acid deposition on freshwaters is that it excludes lakes of <4 ha. Some of these problems will be corrected by second-phase seasonal studies that are under way, but still unreported. The scientific expertise developed under NAPAP would be invaluable in undertaking these tasks, and one hopes that it will still be done.

Did NAPAP Make a Difference?

Despite some very good science, it is difficult to find examples where NAPAP studies greatly changed the world view of acidic precipitation. Few of the predictions made in the 1970s by reputable scientists were altered by NAPAP's findings. Some would dispute this. They state that some scientists in the 1970s were predicting a continued decline in the pH of lakes. With some exceptions (for example, Dillon et al. 1987) this has not happened. But the predictors assumed that sulfur oxide emissions would continue to increase, or at least remain constant. Instead, sulfur oxide emissions have declined, by over 50% in eastern Canada and 25% in the Northeastern U.S. The Clean Air Act of 1970, which took nearly a decade to implement fully, caused industries to begin cutting sulfur emissions, causing lakes to deteriorate less in the 1980s than had been predicted.

How could NAPAP have been done better? In the climate of the early 1970s one would have hoped for a cooperative U.S.–Canada acid rain program that ignored political boundaries and agendas. Designed by the best scientific minds in both countries, it could have resulted in studies of unsurpassed quality for much less money. Logic dictates that problems of international scope require coordinated efforts that are free from restrictions imposed by national boundaries or departments controlled by politicians. Perhaps a "free science agreement" will someday be a part of the negotiations now restricted entirly to free trade in commercial goods.

Is NAPAP a Model for Future Studies?

Yes, if we consider it as an example of how *not* to perform a large-scale assessment. The lesson that throwing a lot of money at science does not buy instant answers or instant excellence/seems to be a hard one for bureaucrats and politicians to learn. The history of NAPAP appears about to repeat itself under the global change banner. Again, the American megaprojects, megaproposals, megacommittees, and megamodels are much in evidence. Once again, reports from specially appointed committees of scientists with expertise peripheral to the problem/are used as an excuse for delaying action until the problem is conclusively proved to exist. Once again, megadollar budgets support computer modelling and remote sensing, with little devoted to real ecology. Unless such large projects can be totally dissected from American politics, I expect a long period of procrastination, accompanied by an expensive, disorderly megascience program controlled by powerful agencies under the thumbs of politicians.

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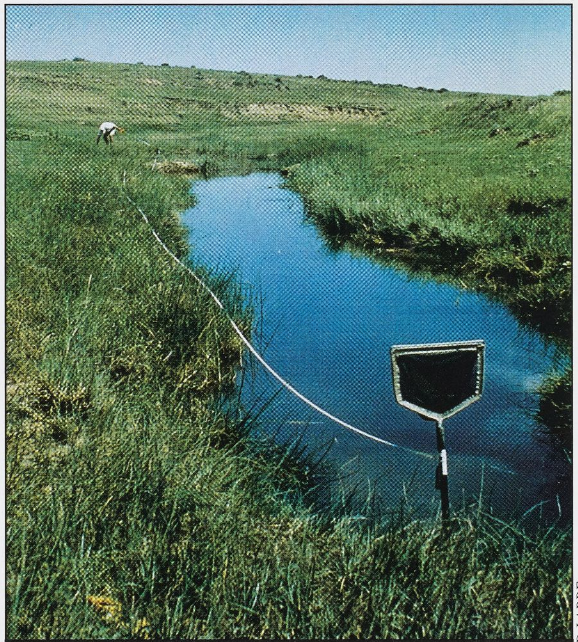
creeks. Based on these surveys over the last 15 years, biologists believe darter populations are not widespread but show signs of stability in limited locations.

What Are We Doing About Darters?

The Division of Wildlife has begun implementing a recovery plan to protect existing Arkansas darter populations and increase their abundance within their historic range. By so doing, the DOW hopes to prevent the species from being listed federally. Biologists launched a two-year research project with Colorado State University to study darter spawning and habitat needs to learn more about water quality and quantity, as well as vegetation, that the species need to survive. The habitat surveys are expected to be completed in 1997.

The Wildlife Commission also adopted new regulations in 1996 that prohibit seining and collecting any fish in natural streams and springs. This regulation is aimed at protecting sensitive fish species, such as the darter, from being collected for commercial bait.

The DOW also has conducted several transplants of Arkansas darters to Fort Carson, the Pueblo Army Depot and Fountain Creek Nature Center. An aggressive program of transplants is underway. The recovery plan also calls for rearing darters at a proposed aquatic native species hatchery with these fish used for future stocking.



Darters have been found at 28 sites in the Arkansas drainage.

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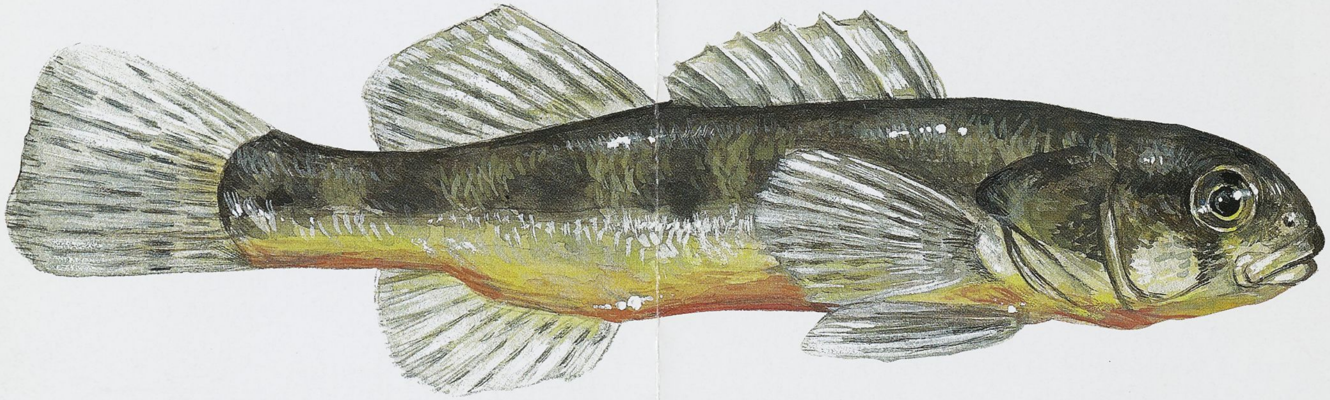
How You Can Help

Habitat protection is the key to ensuring the long-term preservation of Arkansas darters in Colorado. So far, the DOW has transplanted darters in streams along public lands. However, those public streams eventually will be exhausted as potential transplant sites since the majority of darter habitat actually lies within private lands in eastern Colorado.

This is where private landowners can play an important role in working cooperatively with the DOW to recover Arkansas darters. It's in no one's best interest to see the species decline to such a degree that the darter becomes listed as a federally endangered species. Once that happens, federal restrictions could restrict domestic and agricultural uses of water in the Arkansas River drainage.

The DOW is asking landowners and water users to join together in preserving and increasing the populations of Arkansas darters. With sound land and water management practices, this habitat can be protected from overgrazing, development and drying up.

If landowners want to know if they have potential darter habitat on their property or want information about protecting that habitat, the DOW can offer assistance. Just call your local DOW district wildlife manager or the SE Regional Service Center at (719) 473-2945.



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DEFENDING THE DARTER

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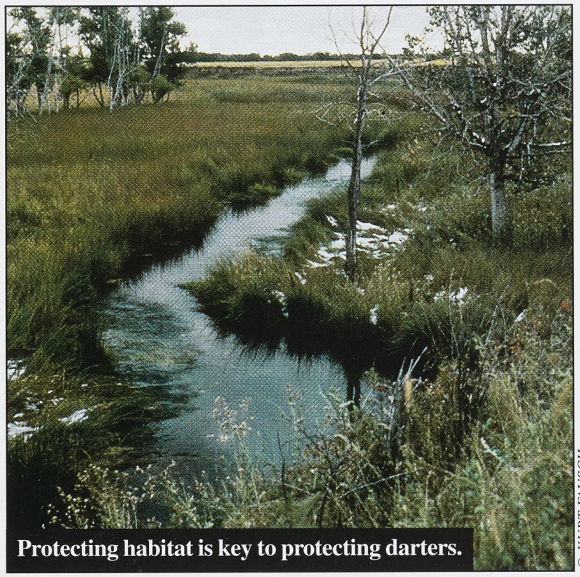
In the late 1800s, streams along the eastern plains and the Arkansas River drainage were inhabited by 25 species of native fish, primarily smaller minnows and perch. The Arkansas darter was one of them. This tiny perch was found in the Arkansas River drainage in southeast Colorado, southern Kansas, northeastern Oklahoma, southwestern Missouri and northwest Arkansas.

However, today the Arkansas darter is scarce in the lower Arkansas River drainage and is listed as a threatened species in Colorado. The Colorado Division of Wildlife is working to protect the darter and make sure it doesn't end up on the federal endangered species list, a designation that implies a precarious status for the species.



Protecting habitat is key to protecting darters.

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Small Perch of Shallow Streams

The Arkansas darter (*Etheostoma cragini*) is a member of the perch family (*Percidae*) that grows no more than 2.5 inches long. This fish has a short, blunt snout with an inconspicuous mouth. It has two dorsal fins, the first a spiny one and the second being soft-rayed, as well as an anal fin with two spines. During breeding season, males turn bright orange along their ventral surface and gill membranes. Females are dark tan with brown-black on their dorsal surface. Both sexes have 12-14 dusky bars along their midsides, a dark wedge-shaped spot below their eyes and undersides covered with tiny dark spots.

Arkansas darters normally are found in small, shallow, clear streams. These are usually spring-fed streams with sandy bottoms, slow currents of cool water and lots of aquatic vegetation, such as watercress. Darters feed on a variety of aquatic insects and some plants, such as small seeds. Mayflies are their main food.

The Arkansas darter is listed as a threatened species in Colorado.

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A Little History About This Little Fish

Scientific information about the Arkansas darter is scant. The earliest historic records show the darters were found around Sell's Lake near Canon City in 1889 and 1913, as well as in a spring-fed arroyo at Lake Station in Lincoln County in 1918. Although little data exists to accurately assess the darters' historic abundance and distribution, fisheries biologists believe that suitable habitat for the species was much more widespread than today. Early records indicate these fish existed as far north as Limon and as far west as Canon City. DOW biologists also point out that early surveys were conducted along mainstem river drainages and transportation lines — places Arkansas darters don't normally live.

Disappearing Darters

The Arkansas darter and its habitat is uncommon. Since the turn of the 20th century, significant changes have likely occurred to the habitat in the lower Arkansas River drainage. Land development, water diversions, reduced water quality and damage of streambank vegetation may have contributed to habitat loss. Stocking non-native fishes and collection of minnows for bait also could be related to the darters' status.

In 1975, the Wildlife Commission listed the Arkansas darter as threatened in Colorado. It is also listed as threatened in Kansas, endangered in Oklahoma and vulnerable in Arkansas. While not listed as threatened or endangered federally, it has been a candidate species since 1987.

Where Are They Now?

Between 1979 and 1981, the DOW surveyed 137 sites in 40 drainages of the lower Arkansas basin. Arkansas darters were found at 12 sites in five counties: El Paso, Elbert, Lincoln, Pueblo and Prowers. Most of the fish were found along Big Sandy, Rush and Fountain creeks. Recently, the DOW completed a three-year plains native fish inventory in 1996, which examined more than 2,000 sites in the Arkansas River drainage. Darters were found at 28 sites in the same five counties with new populations recorded along the Arkansas River, and Antelope, Horse and Fountain

Surveying for Arkansas Darters

© KURT FAUSCH

Robert Behnke

Wild Salmonid Genetics: An Impending Crisis?

In 1991 the American Fisheries Society published a list of 214 stocks of anadromous Pacific Coast salmonids that are already extinct or in various stages of endangerment. Since 1991, four races or stocks of Pacific salmon have been listed for protection under the Endangered Species Act. These include the winter run chinook salmon of the Sacramento River, the spring-summer and fall chinook of the Snake River, and the sockeye salmon of Redfish Lake, Idaho. The American Fisheries Society's publication warning of the precarious state of wild anadromous salmonids of the Pacific Coast stimulated a rash of petitions to list numerous races of Pacific salmon, steelhead, and coastal cutthroat trout for protection under the Endangered Species Act. The sheer number of petitions received contributed to an overload of the system. Many petitions are rejected for lack of information; others pile up in a backlog and will probably never receive adequate reviews.

The perceived urgency of the problem of conserving the genetic diversity of wild salmonid fishes is reflected in a list of priorities prepared by Trout Unlimited's Natural Resource Board at the 1994 annual meeting. Priority number four is "wild salmonid genetics." This is certainly a worthy issue for TU involvement, but I would ask: if one million or ten million dollars were made available to address the issues and problems concerning "wild salmonid genetics," how would it be spent and would the expenditures have any real benefits for conserving the genetic diversity of wild salmonids?

"Genetic research" is a classic example of a nebulous term often resulting in large expenditures with no tangible results. This is because most fisheries biologists and administrators have no more understanding of the subject matter than they do of plasma physics. They lack the understanding necessary to phrase the right questions in need of answers and thus are vulnerable to diverting large amounts of funds to obtain precise answers to irrelevant or wrong questions. Thus, it is basic for the goal of maintaining the genetic diversity of wild salmonids to have credibility, to ask the right questions, and then understand the limitations of any method or technique to answer the question before any method or technique is chosen.

A most important question we must confront was asked in a recent newsletter of the Society for Conservation Biology: "Why do we want to conserve biodiversity, anyway?" The newsletter goes on to point out that conservationists have not been highly successful in getting out our message, such as, why is wild salmonid genetics important? We have a failure in communications at various levels of society. This lack of effective communications became obvious in the outcome of the November 1994 Congressional elections. Helen Chenoweth was elected to represent Idaho in the new Congress. Ms. Chenoweth's environmental platform was essentially provided by the Wise Use Movement. To celebrate her victory, Ms. Chenoweth spoke at an "endangered salmon bake" in Stanley, Idaho (headwaters of the Salmon River, which contains three races of endangered salmon). She asked, "How can I take the salmon's endangered status seriously when you can buy a can at Albertson's?" Such a statement ignores the difference in values between meat in a can and live, wild salmon in a river, and also the fact that the dams that have made live wild salmon so rare in Idaho export most of their benefits outside the state. Her statement does, however, emphasize our failure to communicate on the question, "Why do we want to preserve biodiversity anyway?"

To counter the anti-environmental message in relation to conservation of wild salmonid genetic diversity, two common fallacies should be understood concerning causes of extinction and the "adaptiveness" of intraspecific diversity (genetic diversity within a species). These fallacies were widely propagandized during the last election in one way or another. Their arguments generally follow these lines of reasoning: extinction is a natural process, it is a "built-in" attribute of species to become extinct, and man shouldn't interfere with the laws of nature; and, minor variation among populations and races of a species is nonadaptive, the different parts of a species are interchangeable; therefore, there is no need to save all the parts. The fallacious extinction theory is based on the outdated evolutionary theory of orthogenesis, which presumed a built-in mechanism causing extinction. Modern evolutionary theory has long rejected orthogenesis as lacking any valid basis. In the past, most species became extinct through evolutionary change. That is, they gave rise to new species through time. Their genes were modified and passed on to maintain evolutionary diversity. In contrast, man-induced accelerated extinctions result in termination of evolutionary lines before they can give rise to new species.

The argument against adaptiveness of intraspecific variation is based on the outdated evolutionary theory of early geneticists concerning evolution of new species by "saltation." Genetic mutations were thought of as "macromutations," which could result in a new species in one generation, and "micromutations," which caused the "minor variations" among populations and races of a species. In this theory, Darwinian natural selection, the basis for adaptiveness by slowly perfecting of survival, generation by generation, only played the role of accepting or rejecting the new species arising from a macromutation; "adaptiveness" played no role in the speciation process. Micromutations only supplied the "minor variations" observed within a species and were assumed to be nonadaptive. This theory has also been long rejected by most modern evolutionary geneticists. The fallaciousness of the "saltation" theory of evolution and its associated arguments against adaptiveness of intraspecific diversity has been clearly demonstrated in salmonid fishes. In the 1930s with the beginning of dam building on the Columbia River and blocking of salmon and steelhead runs, it was assumed that the abundance of salmon and steelhead could be maintained by substituting a few generic hatchery stocks for the great diversity of wild populations lost to dams under the mistaken notion of "interchangeable parts." We now realize, too late, that intraspecific diversity (the "minor variations") is indeed adaptive. The sockeye salmon spawning in Redfish Lake and the races of chinook salmon spawning in the headwaters of the Salmon River, Idaho, may show only minor variation in genetic structure to other populations of their species which spawn in rivers near the ocean. The fact that the Redfish Lake sockeye and the Salmon River chinook migrate almost 900 miles from the ocean (adults upstream, smolts downstream) means that they have very different life histories and physiologies compared to other populations of their species. These differences are "adaptive" for their specific spawning environments; they are not interchangeable.

Man-induced extinctions terminate evolutionary lines before they can give rise to new species.

Thus, a goal for the conservation of genetic diversity of wild salmonids would be to preserve the "range of adaptiveness" within a species. For anglers and fisheries managers, prioritizing the types of adaptations we want to preserve and utilize might be based on "trophy" fish. What populations or races have adaptive specializations that result in exceptionally large fish? For example, the world's largest steelhead are produced by populations native to the Skeena River basin. The world's largest chinook salmon are from the Kenai River, Alaska, populations. The world's largest rainbow trout is the Gerrard population of Kamloops rainbow of Kootenay Lake. The world's largest cutthroat trout is the Lahontan cutthroat trout native to Pyramid Lake (*Trout*, Summer 1993). The world's largest brook trout was the coaster population of the Nipigon River (*Trout*, Autumn 1994). Most would agree that these are the types of intraspecific adaptiveness we want to preserve. Let us now return to the issue of wild salmonid genetics and the need to ask the right questions.

All of the examples of important types of adaptations found within species of trout and salmon mentioned above — the longest migrations, the largest size, etc. — have evolved during relatively recent evolutionary times, perhaps about 10,000 years. All of the most modern, state-of-the-art techniques of genetic analysis would find all of these important types of diversity to be quite "insignificant" in terms of their quantitative degree of divergence within their respective species because they have not been separated and isolated for a sufficiently long period of time. The important differences in life history and ecology, the "adaptiveness" of a particular form of trout or salmon, cannot be understood or predicted from the tiny fraction of hereditary material sampled and analyzed by modern genetic techniques. The most important attributes of adaptiveness lie within what is called the regulatory genome, which is not sampled. We can only understand these attributes from observing the life history of an organism.

Thus, I foresee the danger that research on wild salmonid genetics, although of the best intentions, can have a negative influence on the conservation of the most important aspect of genetic diversity — preserving the range of adaptations. This danger will be manifested if people involved in decision-making substitute "data" and quantitative indices for knowledge and critical thinking and fail to ask the right questions.

There are analogies between evaluating and defining significant units of genetic diversity and critical assessment of significance in works of art, literature, and music. Just as artistic critiques require more than a quantitative assessment of colors, notes, and sequences of letters, understanding genetic diversity requires much more than a knowledge of DNA sequences. ■

Fish Culture and Nonindigenous Organisms

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Abstract

Events occurring in 1869, 1870, and 1871 greatly facilitated and promoted the intracontinental dispersal of fishes and other aquatic organisms such as pathogens and parasites as part of public policy in the U.S. Although some view the subsequent results of the massive introductions of nonnative species as "crimes against biodiversity," the issue should be considered in relation to the times in which these introductions occurred. The utilitarian view of nature perceived only benefits resulting from the spread of "good" species beyond their native range. It must also be recognized that nonnative fishes are, overwhelmingly, the basis for inland sport fishing in the West. They have enormous economic value and strong advocacy groups. They are here to stay.

Introduction

Humans appear to have an innate fascination for the exotic. The transplants of "beneficial" plants and animals from one region or another began as soon as trade routes were established. The Vikings may have been in North America 500 years before Columbus but they left no legacy in the form of new world species transplanted into the old world. This legacy began with the voyages of Columbus. There is a common belief that venereal disease pathogens also were transported from the new to the old world, which illustrates that we may get more than we bargain for with transplants of nonnative species and that the most horrendous impacts can be realized from the tiniest packets of DNA. Despite common perceptions, the biggest is not always the baddest.

In nineteenth century America, the benefits of nonnative plants and animals in agriculture were readily apparent. It was only natural then, as public policy, to distribute "good," "valuable" fishes to all parts of the country.

Historical perspective

The completion of the transcontinental railroad in 1869 allowed for relatively rapid transport of live fishes between East and West. The establishment of the American Fish-Culturists' Association (now the American Fisheries Society) in 1870 was the beginning of an influential advocacy group promoting fish culture and the widespread stocking of its products. The creation of the U.S. Fish Commission in 1871 established federal leadership for the rearing and distribution of fishes throughout the country. The transplants of nonnative fishes proceeded rapidly thereafter.

At the annual meeting of the 1872 American Fish Culturists' Association, a resolution recommended "measures be taken to induce the United States to take part in the great undertaking of introducing or multiplying shad, salmon, and other valuable food fishes throughout the country" (Bowen 1970). Although the AFCA was then a small group, they were influential beyond their numbers -- one member, Robert Barnwell Roosevelt, was a U.S. Congressman. Thus, in 1873 the U.S. Fish Commission outfitted a railroad car as an aquarium car (the first of many aquarium cars used to transport fishes around the country). On the East Coast, the aquarium car was loaded with Atlantic lobsters, oysters, and 300,000 marine and freshwater fishes of many species and attached to a train headed for San Francisco. A flood had weakened the trestle across the Elkhorn River, Nebraska. The trestle collapsed, plunging the train with the aquarium car into the flood swollen river (U.S. Fish Comm. 1874:XXIX; Raymond 1990). The first massive introduction of nonnative aquatic organisms by the federal government came to an inglorious conclusion. Undeterred, U.S. Fish Commission employee Livingston Stone, who miraculously escaped drowning in the Elkhorn River, returned to Boston and within a few weeks was on a train to California with shad to stock in the Sacramento River. The shad, *Alosa sapidissima*, is now a common anadromous species along the Pacific Coast, spread far beyond the Sacramento River. In all probability, however, Livingston Stone's heroic effort was not responsible for the establishment of shad on the Pacific Coast. The New York fish culturist, Seth Green, had successfully transported shad to California and stocked them in the Sacramento River in 1871 (Behnke 1990).

The passion and enthusiasm of early fish culturists to spread valuable fishes around the country for the common good is exemplified by an excerpt from Robert Barnwell Roosevelt's presidential address to the 1876 annual meeting of the American Fish Culturists' Association:

> "There is no need to fear of scarcity of food in the ocean or in lakes. This is our national centennial; fish culture has existed only a few years; what will be its condition at its centennial? The most enthusiastic can hardly conceive. A new science was being born into the world -- but the clear light is visible at last. There be no need to fear for the future, and in much less than 100 years the waters of America will teem with food for the poor and hungry which all may come and take."

Roosevelt's wish fulfillment had a King Midas touch -- you get what you want, but it's a disaster. In 1877, the U.S. Fish Commission began the propagation and distribution of common carp, *Cyprinus carpio*, imported from Europe. The carp is now the most abundant freshwater fish in the U.S. in terms of biomass. For fisheries programs in the U.S., as a whole, the carp is the number one pest species and even the poor and hungry don't care to come and take them.

The introduction of common carp also illustrates human faith in technology to improve on nature. Carp were first introduced in America in 1831 by Henry Robinson who obtained them in France and stocked them in ponds along the Hudson River (Bowen 1970). By the 1850's, as expected, some of Robinson's carp had escaped into the Hudson River and became sufficiently abundant to support a commercial fishery. Carp from Germany reached California where they were stocked in a ranch pond in 1872 (Moyle 1976). Thus, carp would have become widely distributed without federal involvement, but the distribution pipeline of the U.S. Fish Commission ensured their introductions into every major drainage basin in the country. The U.S. Fish Commission was aware that carp had long been established in the U.S. but it was thought that these earlier introductions were of the "inferior" wild variety. The 1877 importation by the U.S. Fish Commission consisted of selectively bred domesticated varieties which were thought to be far superior to wild fish.

The impact of nonnative fishes on native species has been especially severe west of the Continental Divide where native species were relatively few (highly unsaturated fish faunas, especially in the arid Southwest) and most of the favorite sport fishes of the families Centrarchidae (bass, sunfishes), Percidae (perch, walleye), Ictaluridae (catfishes), and Esocidae (pike) are not native. Also, the era of reservoir construction and river regulation created new, artificial environments for which most native fishes are ill-adapted -- new niches to be filled by nonnative species.

The native fish fauna of the upper Colorado River basin consists of 13 species. Currently, 40 species have been recorded from the upper basin, 27 of which are nonnative. Four of the native species, Colorado squawfish, *Ptychocheilus lucius*, razorback sucker, *Xyrauchen texanus*, humpback chub, *Gila cypha*, and bonytail, *G. elegans*, are federally endangered (Behnke and Benson 1980 and subsequent updating). Miller et al. (1989) reported 26 species and subspecies of North American freshwater fishes to be extinct. Most extinctions are attributed to nonnative species introductions (see Courtney and Stouffer 1984, and Minckley and Deacon 1991 for comprehensive documentation of impacts and extinctions caused by nonnative fishes).

The U.S. Fish Commission and its successors, the U.S. Bureau of Fisheries and the U.S. Fish and Wildlife Service, cooperated with other countries to ship "valuable" American fishes to foreign lands. Rainbow trout, *Oncorhynchus mykiss*, and to lesser extents, brook trout, *Salvelinus fontinalis*, lake trout, *S. namaycush*, and Atlantic salmon, *Salmo salar*, were stocked in most cold water environments of the world, especially in the Southern Hemisphere where no fishes of the family Salmonidae are native. The establishment of nonnative trout in South America and New Zealand have created world famous fishing attracting hordes of foreign anglers and associated economic benefits. Although nonnative salmonid species are certainly not benign in their impacts on native species in foreign lands, I know of no case of extinction of a species caused by introduced salmonids. Largemouth bass, *Micropterus salmoides*, an aggressive warmwater predator, on the other hand, can have a devastating impact on native species, especially if the native fishes had evolved in the absence of a relatively large predatory fish. Lake Lanao, Mindanao Island of the Phillippines, has often been cited as an example of "explosive speciation" of a species flock of cyprinid fishes. Supposedly, a single ancestor gained access to the lake and radiated into 18 species classified in four genera. In 1915, General John Pershing, leader of U.S. occupation troops in the Phillippines, had largemouth bass shipped and stocked into Lanao. Few of the endemic species can now be found (Kornfield and Carpenter 1984) -- an example of biological imperialism.

Current Realities

Courtenay and Moyle (1992) published a paper entitled "Crimes against biodiversity: the lasting legacy of fish introductions." The obvious implication is that crimes are committed by criminals. Indeed, today it would be a criminal act to deliberately introduce largemouth bass into a refuge pond holding a federally endangered species. From an historical perspective, however, I can't consider the pioneer fish culturists of the late nineteenth century who so zealously propagated and transported fishes about like Johnny Appleseed, as criminals. They acted as directed to carry out the public policy of their times.

There is now considerable public awareness of dangers posed by nonnative organisms such as zebra mussels, brown tree snakes, and whirling disease in trout. The era of indiscriminate, deliberate introductions of new nonnative aquatic species as public policy is over, but the horse is out of the barn; it is too late to close the door and in most situations there is really not much that can be done to correct past mistakes, except on a very limited scale.

The most pervasive contemporary negative impact on native fishes from fish hatcheries and stocking as government policy concerns intraspecific impacts of stocking massive numbers of anadromous salmonids, especially coho salmon, *Oncorhynchus kisutch*, chinook salmon, *O. tshawytscha*, and steelhead, *O. mykiss*. The hatchery stocks propagated are rarely native to the rivers where they are stocked (most hatchery stocks are a mixture of several parental populations) and have undergone varying degrees of artificial selection. Hatchery juveniles compete with wild native juveniles, lowering survival. Intensive fisheries on adults do not discriminate between hatchery and wild fish, leading to over-exploitation of wild fish. Hatchery fish escaping to spawn with wild fish results in "outbreeding depression" because the life history of the nonnative hatchery fish is mismatched to the precise site-specific environments where native populations have long coevolved and coadapted.

In 1990 a petition was submitted to list the coho salmon of the lower Columbia River basin for protection under the Endangered Species Act. The National Marine Fisheries Service rejected this petition because they could not find any "pure" native populations of coho -- they had been "homogenized" and replaced by the many millions of coho stocked each year from hatcheries. Similar situations exist with most coho populations of the coastal rivers of Oregon and Washington. Flagg et al. (1995) documented the massive scale of hatchery propagation of coho and the mixing of many parental stocks to produce "generic," homogenized hatchery stocks which lack site-specific adaptiveness to any river. Wild, truly native coho populations are now extremely rare in Pacific Coast rivers of the U.S.

Nelson and Bodle (199) documented the extinction of the native population of chinook salmon in the Little White River, Washington, from the operation of a fish hatchery on the river.

The controversy concerning preservation of native races of anadromous salmonids and impacts of hatchery programs propagating and stocking hundreds of millions of "nonnative" fish is heating up as the plight of the wild, native fish becomes better understood. Attempts to maintain salmon abundance by dependence on hatcheries was characterized by Meffe (1992) as "techno-arrogance and halfway technologies." In 1995, the National Research Council released a draft summary of a report, "Upstream: salmon and society in the Pacific Northwest," which concludes that hatcheries have not only failed to reverse declines in abundance of salmon and steelhead, they have inadvertently contributed to it. A feature article on the controversy appeared in the May 12, 1996 edition of *The Seattle Times.*

A basic problem for resolving the conflict over fish hatcheries and their intraspecific negative impacts on wild native races of anadromous salmonids is that these state, federal, and tribal hatcheries represent over a billion dollars of capital investment and directly or indirectly provide employment for thousands of honest, hard-working people. Our naive faith in technological fixes to improve on nature is on a collision course with evolutionary reality in regards to preserving the biodiversity of anadromous salmonids. There is no simple solution to this dilemma.

In summary, environmental and conservation issues generated by nonindigenous aquatic organisms can cause considerable polarization between the anthropocentric, utilitarian, self-interest point of view of "good, bad, and indifferent" species irrespective of their status as native or nonnative, and the ecocentric point of view of good (native) and bad (nonnative) species. In the West, most sport fishing is dependent on nonnative fishes. Much of this angling occurs in "nonnative" or artificial environments of reservoirs and regulated rivers (tailwaters) where there is no possibility of continued existence of coevolved and coadapted native fish faunas.

The Office of Technological Assessment of the U.S. Congress issued a report on nonindigenous species in 1993. A succinct and insightful conclusion was that some have profound environmental effect, but nonnative species are here to stay....and many are welcome. Indeed, this is true in regards to nonnative sport fishes with their strong advocacy groups and associated socio-political and economic ramifications.

A common ecocentric viewpoint often expressed in frustration over nonnative species problems goes something like this: *If there were only a magic button to be pushed that would eradicate all nonnative species, I would not hesitate to push it.* If this button-pusher were an employee of a state or federal agency, could they get away with it? Considering issues such as "public good" and the "will of the people" as interpreted by Congress and state legislatures, it is likely our hypothetical button-pusher would be unemployed and charged with criminal activity.

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SWEET DEAL

WHY ARE THESE MEN SMILING? THE REASON IS IN YOUR SUGAR BOWL

OCCUPYING A BREATHTAKING SPOT on the southeast coast of the Dominican Republic, Casa de Campo is one of the Caribbean's most storied resorts. It bills itself as "a hedonist's and sportsman's dream," and that's truth in advertising. The place has 14 swimming pools, a world-class shooting ground, PGA-quality golf courses and $1,000-a-night villas.

A thousand miles to the northwest, in the Florida Everglades, the vista is much different. Chemical runoff from the corporate cultivation of sugar cane imperils vegetation and wildlife. Polluted water spills out of the glades into Florida Bay, forming a slimy, greenish brown stain where fishing once thrived.

Both sites are the by-product of corporate welfare.

In this case the beneficiaries are the Fanjul family of Palm Beach, Fla. The name means nothing to most Americans, but the Fanjuls might be considered the First Family of Corporate Welfare. They own Flo-Sun Inc., one of the nation's largest producers of raw sugar. As such, they benefit from federal policies that compel American consumers to pay artificially high prices for sugar.

Since the Fanjuls control about one-third of Florida's sugar-cane production, that means they collect at least $60 million a year in subsidies, according to an analysis of General Accounting Office calculations. It's the sweetest of deals, and it's made the family, the proprietors of Casa de Campo, one of America's richest.

The subsidy has had one other consequence: it has helped create an environmental catastrophe in the Everglades. Depending on whom you talk to, it will cost anywhere from $3 billion to $8 billion to repair the Everglades by building new dikes, rerouting canals and digging new lakes.

JIM VIRGO—FORT LAUDERDALE SUN-SENTINEL

SUBSIDY BARONS: Alfonso, left, and Jose Fanjul at the Palm Beach offices of their Flo-Sun Inc., a major sugar producer

Growers are committed to pay up to $240 million over 20 years for the cleanup. Which means the industry that created much of the problem will have to pay only a fraction of the cost to correct it. Government will pay the rest. As for the Fanjuls, a spokesman says they are committed to pay about $4.5 million a year.

How did this disaster happen? With your tax dollars. How will it be fixed? With your tax dollars.

It is not news that sugar is richly subsidized, or that the Fanjuls have profited so handsomely. Even as recently as 1995, when Congress passed legislation to phase out price supports for a cornucopia of agricultural products, raw sugar was spared. Through a combination of loan guarantees and tariffs on imported sugar, domestic farmers like the Fanjuls are shielded from real-world prices. So in the U.S., raw sugar sells for about $22 a pound, more than double the price most of the world pays. The cost to Americans: at least $1.4 billion in the form of higher prices for candy, soda and other sweet things of life. A GAO study, moreover, has estimated that nearly half the subsidy goes to large sugar producers like the Fanjuls.

A spokesman for Flo-Sun, Jorge Dominicis, said the company disagrees with the GAO's estimate on the profits the Fanjuls and other growers derive from the program.

"That is supposed to imply somehow that our companies receive $60 million in guaranteed profits," he said, "and that is flat-out not true. Our companies don't make anywhere near that kind of profit."

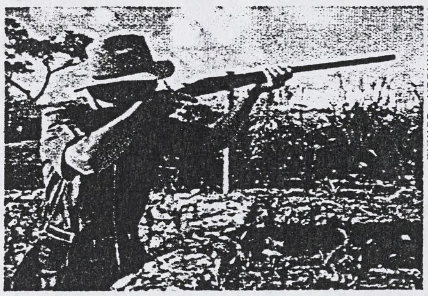
Dominicis, like other proponents of the sugar program, contends that it doesn't cost taxpayers a penny and is not unlike government protection of other American industries. "If our [sugar policy] is corporate welfare, which I don't believe it is, then all trade policy is corporate welfare," he says.

Flo-Sun is run by four Fanjul brothers, Alfonso ("Alfie"), Jose ("Pepe"), Andres and Alexander. Their family dominated Cuba's sugar industry for decades, and they came to this country with their parents in 1959, after Fidel Castro seized power. The Fanjuls arrived just as a U.S. Army Corps of Engineers project to control the flow of water in the Florida Everglades made large-scale development possible.

arents tell of children who have been "leaded" by the nearby smelter

The total acreage planted in sugar cane there soared—from 50,000 acres in 1960 to more than 420,000 today.

Within that swampy paradise lies yet another subsidy. Each year, according to a 1997 estimate, the Army Corps of Engineers spends $63 million to control water flow in central and south Florida. This enables growers to obtain water when they need it or restrain the flow during heavy rains. Of the $63 million, the Corps estimates $52 million is spent on agriculture, mainly sugar-cane farmers, in the Everglades.



TONY ARRUZA—CORBIS

CASA DE CAMPO: The Fanjuls' luxurious resort features grouse hunting, polo, 14 swimming pools—and more

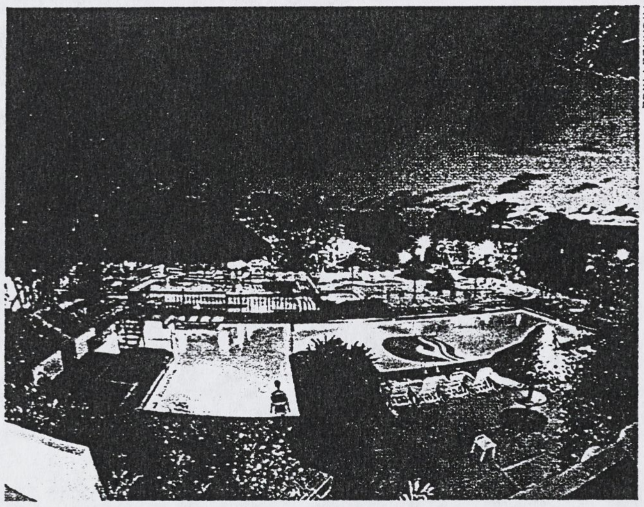
Even with the additional production from the Glades, propped up by price supports, the U.S. can't produce all the sugar it needs. The Federal Government rations access to the lucrative U.S. market by assigning quotas to 40 sugar-producing nations, most of them developing countries. And, remarkably, the Fanjuls have found riches here too. Every year, the country that receives the largest sugar quota is the Dominican Republic. With a per-capita income of $1,600 a year and an unemployment rate hovering around 20%, that Caribbean nation needs all the economic help it can get. And who is the largest private exporter of Dominican sugar? The Fanjuls, thanks in part to their long-standing relationship with the Dominican Republic's politicians. Through a subsidiary, Central Romana Ltd., the brothers grow sugar cane and operate the world's largest sugar mill there. The profit margin is substantial, partly because cane cutters on the island earn about $100 a month, making production costs much lower than in Florida. From their Dominican plantation the Fanjuls export roughly 100,000 tons of raw, duty-free sugar each year to the U.S.

Whether they sell sugar from their holdings in the Everglades or from their mill in the Caribbean, the Fanjuls are guaranteed a U.S. price that is more than double anywhere else in the world. As might be expected, having it both ways has propelled the Fanjuls into the ranks of the richest Americans. Their wealth is counted in the hundreds of millions of dollars.

And although they appear frequently in the society pages, the Fanjuls won't be caught dead in the financial section. As Emilia Fanjul, the wife of Pepe, once confided to a society reporter, "We like to be private about the business."

Depending on the season, the Fanjuls can be found shooting game in Scotland, skiing in Switzerland or relaxing at their spectacular Casa de Campo. These 7,000 acres overlooking the sea have long been a favorite playground of the wealthy. But Palm Beach is still their real home, and Florida is still the heart of their financial empire. They now farm an estimated 180,000 acres of cane-producing land in the Everglades—43% of the total—making them one of the two-largest sugar growers in the state.

For decades, this region has been home to one of the worst jobs in America—hacking cane with a machete. Until the work was mechanized in the 1990s, the growers had to bring in thousands of cane cutters from the Caribbean every season. Yet in preserving the subsidy that has made millionaires of the Fanjuls, Congress has cited the fact that it saves American jobs.



MICHAEL PRICE

Migrant-labor organizations and legal-aid groups in Florida have long waged an ongoing battle with the Fanjuls and other growers over the abysmal conditions. Greg Schell, an attorney with the Migrant Farmworkers Justice Project in Belle Glade, Fla., contends that of all the growers, the Fanjuls have treated their workers the worst. "They are in a class by themselves," he said. A lawsuit seeking back wages and benefits is expected to go to trial next spring.

Every few years, critics of the sugar program attempt to roll back the subsidy that has enriched the Fanjuls and kept sugar prices high. And every time they fail, largely because of the power of the sugar lobby, which includes not just large growers like the Fanjuls but thousands of small sugar-beet farmers in other parts of the nation.

Though by no means the largest special interest in Washington, the sugar lobby is one of the most well-heeled. And among growers, the Fanjuls are big givers. Family members and corporate executives have contributed nearly $1 million so far in this decade, dividing the money fairly evenly between political parties.

This knack for covering all political bases carries all the way to the top of the Fanjul empire. Alfonso Fanjul served as co-chairman of Bill Clinton's Florida campaign in 1992. His brother Pepe was national vice chairman of finance for Bob Dole's presidential campaign in 1996 and was host to a $1,000-a-head fund raiser for Dole at his Palm Beach mansion. After Clinton's 1992 victory, Alfie was a member of the select group invited by the Clinton camp to attend the President-elect's "economic summit" in Little Rock, Ark.

Careful readers of Kenneth Starr's impeachment report to Congress will note that on Feb. 19, 1996, Alfie called President Clinton while the President was closeted with Monica Lewinsky in an emotional meeting in the Oval Office. After breaking the news that "their intimate relationship" would have to end—temporarily, as it turned out—the President returned Fanjul's call; Lewinsky left. The two spoke for 22 minutes. The topic: a proposed tax on sugar farmers to pay for the Everglades cleanup. Fanjul reportedly told the President he and other growers opposed such a step, since it would cost them millions. Such a tax has never been passed.

That's access. ■

The subsidy that wouldn't die: why we pay double for sugar

Ecosyst. health / benefits / Arbor Day, ND

functions

FISH BITES

• September 16 was the cutoff date for public comments on a proposed interim rule that would release certain activities such as fishery harvest, hatchery management, habitat restoration, and research from the Endangered Species Act "take" regulations on coho salmon in southern Oregon and northern California if the National Marine Fisheries Service (NMFS) agreed the activities were regulated consistently with the Oregon Coastal Salmon Restoration Initiative. An interim rule that aims to protect threatened coho salmon stocks during establishment of a final rule by NMFS went into effect 18 August. At press time, the agency planned to reconsider and possibly amend the rule after the comment period closed. For information call Garth Griffin, 503/231-2005.

• Three recent studies conclude that natural diversity by itself does not ensure healthy ecosystems. Scientists who studied ecological diversity in California, Sweden, and Minnesota found that it "often had little bearing on the performance of ecosystems—at least as measured by the growth and health of native plants," according to an article in *The Washington Post*. Oddly, the studies found that ecosystems with the broadest biological diversity were often the weakest in productivity and nutrient cycling. However, scientists agreed that in areas with the greatest species diversity such as rainforests broad species variation seems to be critical to the ecosystem's adaptability to environmental changes.

• At press time, leaders involved in the politics of salmon management were arriving in Seattle, Washington, for the 13 September Salmon Homecoming Forum to discuss U.S.-Canadian negotiations of the Pacific Salmon Treaty and other related issues. For information on materials emerging from the meeting, call For the Sake of the Salmon, 503/650-5447.

• Obtaining information about recreational-fishing-trip-related expenses, satisfaction, viewing sites, and attitudes toward resource management is among a new set of recommendations for the Atlantic Coastal Cooperative Statistics Program socioeconomic data collection program that is being proposed by the Committee on Economics and Social Sciences, Atlantic States Marine Fisheries Commission. Under the recommendations, separate socioeconomic data collection programs will be developed for commercial and recreational fisheries. The new programs aim to integrate human elements into fisheries management. For information contact Bob Beal, 202/289-6400, ext. 332.

• Tunas, sharks, and swordfish may be managed under a single fishery management plan, although billfish would continue to have its own management system, according to the National Marine Fisheries Service. The agency has until 11 October to alter all fisheries management plans to comply with standards outlined in the Sustainable Fisheries Act regarding overfishing, rebuilding stocks, and reducing bycatch.

• A report to Congress regarding ecosystem approaches to marine fisheries conservation will be completed by October 1998. A National Marine Fisheries Service's Ecosystem Principles Advisory Panel, a group of 20 experts, will examine how marine ecosystem research is conducted and advise the agency regarding how such findings "can and should be used to improve marine fisheries management," according to the National Center for Marine Conservation, which serves on the panel.

MEMBERS: Submit Fisheries News items to Kristin Merriman-Clarke, 301/897-8616, ext. 220, kclarke@fisheries.org.

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Salmonid phylogeny inferred from ribosomal DNA restriction maps

R. B. Phillips, K. A. Pleyte, and M. R. Brown

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Salmonid Phylogeny Inferred from Ribosomal DNA Restriction Maps

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Phillips, R. B., K. A. Pleyte, and M. R. Brown. 1992. Salmonid phylogeny inferred from ribosomal DNA restriction maps. Can. J. Fish. Aquat. Sci. 49: 2345–2353.

Genomic DNA was isolated from 17 salmonid species including six species of *Salvelinus* (*S. namaycush*, *S. fontinalis*, *S. leucomaenis*, *S. confluentus*, *S. malma*, and *S. alpinus*), two species of *Salmo* (*S. trutta* and *S. salar*), eight species of *Oncorhynchus* (*O. mykiss*, *O. clarki*, *O. masou*, *O. tshawytscha*, *O. kisutch*, *O. keta*, *O. nerka*, and *O. gorbuscha*), and one species of *Hucho* (*H. perryi*). Restriction maps of the ribosomal DNA were prepared by using probes to the 18S and 28S coding regions of the rDNA. Phylogenies were constructed from this data using both cladistic and distance methods. Results supported the recent placement of the Pacific trouts in the genus *Oncorhynchus*. The phylogeny obtained for the genus *Salvelinus* suggested that *S. confluentus* from North America may be more closely related to *S. leucomaenis* from Japan than to species in the *S. malma* – *S. alpinus* complex. Fixed differences in restriction sites were found among the major subgroups within the *S. malma* – *S. alpinus* complex.

Nous avons isolé l'ADN génomique de 17 espèces de salmonidés incluant six espèces de *Salvelinus* (*S. namaycush*, *S. fontinalis*, *S. leucomaenis*, *S. confluentus*, *S. malma*, et *S. alpinus*), deux espèces de *Salmo* (*S. trutta* et *S. salar*), huit espèces de *Oncorhynchus* (*O. mykiss*, *O. clarki*, *O. masou*, *O. tshawytscha*, *O. kisutch*, *O. keta*, *O. nerka*, et *O. gorbuscha*), et une espèce de *Hucho* (*H. perryi*). Nous avons préparé des cartes de restriction de l'ADN ribosomique en utilisant des sondes moléculaires correspondant aux régions de l'ADNr codant pour l'ARNr 18S et 28S. À partir de ces données, nous avons construit des relations phylogénétiques en utilisant des méthodes tant cladistiques que de distance. Les résultats corroborent l'inclusion récente des truites du Pacifique dans le genre *Oncorhynchus*. L'étude phylogénétique du genre *Salvelinus* semble indiquer que l'espèce *S. confluentus* d'Amérique du Nord peut être plus étroitement apparentée à l'espèce *S. leucomaenis* du Japon qu'aux espèces du complexe *S. malma* – *S. alpinus*. On a retrouvé des différences fixes entre les sites de restriction des principaux sous-groupes du complexe *S. malma* – *S. alpinus*.

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The subfamily Salmoninae includes six genera of trouts, salmons, and charrs: *Brachymystax*, *Hucho*, *Salmothymus*, *Salvelinus*, *Salmo*, and *Oncorhynchus*. These fishes have been the subjects of numerous taxonomic studies using morphological (Norden 1961; Behnke 1965, 1980, 1989; Cavender 1978, 1980; Cavender and Kimura 1989; Smith and Stearley 1989; Stearley 1990), karyological (reviewed in Hartley 1987; Phillips et al. 1989a, 1989b), ontogenetic (Balon 1980; Pavlov 1980; Kendall and Behnke 1984), allozyme (Tsuyuki and Roberts 1966; Utter et al. 1973; Johnson 1984), and mitochondrial DNA markers (Thomas et al. 1986; Gyllensten and Wilson 1987; Ginatulina et al. 1988; Grewe et al. 1990). However, there are a number of unresolved problems. Major areas of uncertainty involve the relationships of the three more primitive genera to the others, and the relationships among the species in the genus *Salvelinus* and among the species in the genus *Oncorhynchus* (reviewed in Phillips and Pleyte 1991). Although the three primitive genera *Brachymystax*, *Hucho*, and *Salmothymus* are found only in Europe and Asia, a Miocene fossil species, *Paleolox larsoni*, which shares many features with *Hucho* and some with *Salvelinus*, has been found in Idaho (Smith et al. 1982).

In the case of the species in the genus *Salvelinus*, the phylogenetic trees based on allozyme and mtDNA data are different from the ones based on osteological data, and unresolved branches remain in all of the trees. For species in the genus *Oncorhynchus*, the tree based on mtDNA conflicts with the trees based on allozymes and osteological data. From the theoretical point of view, one would expect DNA sequence comparisons to be more useful than protein allozymes for phylogenetic analysis, especially in the tetraploid salmonid species. However, it has been shown that maternally inherited mtDNA can "invade" the genome of related species (Ferris et al. 1983) so that a phylogeny based on mtDNA alone may be incorrect. It is likely that hybridization between the various salmonid species has been common in the past, so that examination of nuclear DNA sequences is essential for a more complete systematic analysis.

The nuclear ribosomal RNA genes (rDNA) are especially suitable for use in phylogenetic analysis, as there are three types of regions that evolve at different rates (see Fig. 1). The coding regions for the 5.8S rRNA, the 18S rRNA, and most of the 28S rRNA evolve slowly and can be used in comparisons of distantly related species. The internal and external transcribed spacer regions (ITS-1, ITS-2, 3′ETS, and 5′ETS) as well as

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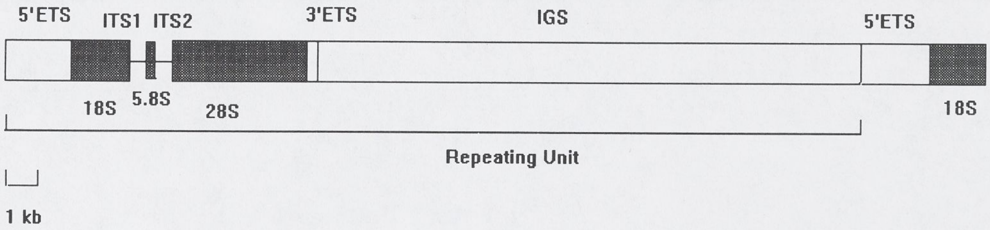

FIG. 1. Diagram showing the structure of the ribosomal RNA genes in eukaryotes. The 5.8S, 18S, and 28S are the regions coding for the 5.8S, 18S, and 28S rDNAs. The ITS-1 and ITS-2 are the internal transcribed spacer regions, the 5′ETS and the 3′ETS are the external transcribed spacer regions, and the IGS is the intergenic spacer region between the repeating units.

the expansion segments of the 28S rRNA evolve more rapidly and can be used in comparison of more closely related species. The intergenic spacer region (IGS) evolves very rapidly and can be used in comparisons of subspecies or populations within a species. Restriction maps of the entire rDNA repeating unit have been used successfully for phylogenetic analysis in several taxa (Coen et al. 1982; Wilson et al. 1984). For example, data obtained from rDNA restriction maps in 32 species of *Rana* that last shared a common ancestor 50 million yr ago have provided an independent test of the previous phylogenetic hypothesis based on allozymes and morphology (Hillis and Davis 1986). In this paper, we present a phylogenetic analysis of restriction site data on the nuclear ribosomal DNA in salmonid fishes of four genera: *Hucho, Salvelinus, Salmo*, and *Oncorhynchus*.

Materials and Methods

Tissue samples were obtained from individuals of 17 different species, with at least two geographically distinct populations sampled for all of the species except those native to Japan and *O. clarki* and *O. mykiss* (Table 1). In the case of *S. alpinus*, at least two populations were sampled from each of the three major subspecies proposed by Behnke (1984): *S. alpinus alpinus* from Europe, *S. alpinus erythrinus* from the high Arctic, and *S. alpinus ''taranetz''* from the Chukokst–Bering Sea region.

Genomic DNA was extracted from fish livers by phenol extraction (Popodi et al. 1985). The restriction enzymes used in this study included the following enzymes which recognize six base sequences: ApaI, BamHI, BclI, BglII, DraI, EcoRI, HindIII, KpnI, NheI, PstI, PvuII, SspI, SstI, XbaI, and XhoI. Restriction enzyme digestions were carried out at 37°C as recommended by the supplier (BRL). Following digestion, samples were separated by electrophoresis for 17 h at 35 V in 0.6% agarose and transferred to a nylon filter (Zeta-bind) as described by Southern (1975). Filters were baked for 2 h at 80°C. Prehybridization was done for 2 h at 65°C in the following solution: 1% BSA, 7% SDS, 500 mM sodium phosphate (pH 7.0), and 1 mM EDTA. Hybridization was done in the same solution overnight at 65°C, and posthybridization washes of filters were carried out at 65°C. Two washes were done for 15 min in 0.5% BSA, 5% SDS, 40 mM sodium phosphate (pH 7.0), and 1 mM EDTA and then two more without the BSA. Filters were sequentially hybridized with radioactive probes to rDNA from mouse and Chinese hamster ovary. Clone I-19 was a 4.2-kb Eco RI-SalI fragment containing most of the 28S rDNA coding region from mouse cells and clone PEB-4 was a 1.9-kb Eco RI-SalI fragment containing most of the 18S coding region from Chinese hamster ovary cells. Probes were made radioactive using the random primer reaction according to the manufacturers's instructions (Pharmacia). Filters were dried and exposed to X-Omat film (Kodak) at −70°C with an intensifying screen (DuPont-Cronex).

Genomic DNA from a minimum of three individuals per species was digested singly with each of the 15 enzymes listed above and appropriate double digestions were done to confirm homologies of restriction sites and to construct restriction site maps of the rDNA for each species.

There were two types of variable restriction sites: those which were either present or absent in a given individual (+/− sites) and those which exhibited intraindividual length polymorphisms so that a given individual had a cluster of closely spaced bands spanning a region of a few kilobases (Phillips and Pleyte 1991). Almost all of the sites in the IGS exhibited intraindividual variation, but it was never found for sites in the coding regions or transcribed spacer regions 5′ETS and ITS. In different species, these band clusters were usually either absent or present, but clusters of bands in a couple of different size ranges were found for two enzymes. In the phylogenetic analysis, these sites were considered different between species if the size ranges of the band clusters did not overlap. The +/− sites found in more than one species did not show intraspecific variation with the exception of one site (ApaI in the 5′ETS) which was not used in the interspecific phylogenetic analysis. F1 hybrids between *S. fontinalis* and *S. confluentus* had the banding patterns expected for the +/− sites which exhibited differences in the parental species (Phillips and Pleyte 1991).

The restriction site data were analyzed first as discrete characters. Informative sites (those in which two or more taxa contained the restriction site and two or more taxa lacked the restriction site) were identified and phylogenetic trees were constructed using the maximum parsimony method of Swofford's PAUP program (Swofford 1985) for the species in the genus *Salvelinus, Salmo*, and *Oncorhynchus* using *H. perryi* as an outgroup. Trees were also obtained for the *Salvelinus* species and *H. perryi* with *Salmo* as an outgroup and for the *Oncorhynchus* species with *Salmo* as an outgroup. The data were bootstrapped using 100 replications.

The proportions of nucleotide differences for each pair of species were also computed. The maximum likelihood estimates of the number of nucleotide differences per site (d) between each pair of species were calculated following Nei and Tajima (1983) and divergence estimates between taxa are reported as percent sequence divergence. These data were used to construct distance phenograms using the UPGMA (Sneath and Sokal 1973), neighbor joining (Saitou and Nei 1987), and Fitch–Margoliash (Fitch and Magoliash 1967) (FITCH) methods of the PHYLIP computer program.

TABLE 1. Taxa used in this study and their origin.

Species	No. of fish[a]	Origin
Hucho perryi (Japanese huchen)	2	Hokkaido Fish Hatchery, Japan, 1988
Salvelinus		
S. leucomaenis (Iwana)	6	Hokkaido Fish Hatchery, Japan, 1988
S. fontinalis (brook trout)	4	Dep. Nat. Resour., St. Croix, WI, 1986
	2	Ont. Minist. Nat. Resour., Maple, Ont., 1986
S. namaycush	24	Seneca Lake, NY, 1986
(lake trout)	24	Gull Island Shoals, Bayfield, WI, 1987, 1988
	24	Iron River, MI (Marquette stock), 1987
	24	Jenny Lake, WY, 1987
S. confluentus	4	Arrow Lake, B.C., 1990
(bull trout)	2	Gold Creek, ID, 1990
S. malma	2	Fox River (Kenai), AK, 1988
(Dolly Varden)	3	Auke Creek, AK, 1989
	4	Noatak River, AK, 1990
S. alpinus (Arctic char)	4	Freshwater Inst., MN (Nauyuk Lake, N.W.T.), 1986
	2	Freshwater Inst. (Storvaln, Norway), 1986
	20	Loch Rannoch, Scotland, 1987, 1990
	3	East Finger Lake, AK, 1987
	8	Dolly Varden Lake, AK, 1987
	6	Bangor, ME, 1988
Salmo		
S. trutta (brown trout)	6	Dep. Nat. Resour., St. Croix, WI, 1986
S. salar	3	River Spey, Scotland, 1987
(Atlantic salmon)	3	River Tweed, Scotland, 1987
	4	Grey River, Nfld., 1989
Oncorhynchus		
O. mykiss (rainbow trout)	6	Wisc. Dep. Nat. Resour. (Shasta), 1986
O. clarki (cutthroat trout)	4	Yellowstone Lake, MT, 1990
O. masou (masu salmon)	6	Hokkaido Fish Hatchery, Japan, 1988
O. tshawytscha	6	Kitimat River, B.C., 1989
(chinook salmon)	6	Warm Springs, WA, 1989
O. kisutch	6	Kewaunee River, WI, 1989
(coho salmon)	6	Auke Creek, AK, 1989
O. keta	6	Yukon River, AK, 1988
(chum salmon)	6	Bristol Bay, AK, 1988
O. nerka	2	Cook Inlet, AK, 1988
(sockeye salmon)	2	Bristol Bay, AK, 1989
	12	Mission Creek, B.C., 1990
O. gorbuscha (pink salmon)	6	Prince William Sound, AK, 1987, 1989
	6	Sitka, AK, 1987, 1989
	4	Auke Bay, AK, 1988, 1989
	6	Gastineau Hatchery, Juneau, AK, 1989
	8	Paratunka River, Russia, 1989
	4	Utka River, Russia, 1990

[a]Three from each stock were examined for all enzymes, and the additional individuals were examined for enzymes showing polymorphic bands.

Results

Interspecific Variation

Seventy-eight restriction sites in the rDNA were mapped among the 17 species (Fig. 2; Tables 2 and 3). The summary of conserved and variable sites (Table 3) indicates that almost all of the conserved sites were in the coding regions. In Fig. 2 the conserved sites are shown below the map and the phylogenetically informative sites are shown above the map. The 5′ETS and the IGS contained the most informative sites.

A cladistic analysis of the six *Salvelinus* species with the branch and bound option of PAUP using *H. perryi* as the outgroup revealed only one tree of minimal length (Fig. 3). When these data were subjected to bootstrapping, none of the branches was found with greater than 90% confidence limits.

When a similar cladistic analysis was done with the *Oncorhynchus* species using *Salmo* as an outgroup, nine trees were found. The consensus tree is shown in Fig. 4. The trees were similar in overall topology, with the differences occurring in the placement of *O. keta* with respect to the other Pacific salmon and in the placement of *O. masou* with respect to the Pacific trouts and North American Pacific salmon. There were three different topologies for *O. keta* and three different topologies for *O. masou*. *Oncorhynchus masou* was clustered with *O. clarki* and *O. mykiss* in one tree, on a branch between the Pacific trouts and Pacific salmon in another tree, and in a trichotomy with the other two groups in the third tree. In all of the trees, *O. kisutch* and *O. tshawytscha* were placed together and *O. gorbuscha* and *O. nerka* were together. In one of the trees, *O. keta* was placed closer to *O. kisutch* and *O. tshawytscha*, in a second tree, it was placed on a separate branch from the other species, and in the third tree, it was placed exactly in the middle between the two sister groups. When the North American Pacific salmon species were analyzed using *O. masou* as an outgroup, the same trees were obtained for these five taxa. The results of bootstrapping indicated that the branch leading to *O. kisutch* and *O. tshawytscha* was obtained 87% of the time and the branch leading to *O. nerka* and *O. gorbuscha* 63% of the time (Fig. 4). When all 17 taxa were analyzed together with *H. perryi* as the outgroup, *O. masou* clustered with *O. clarki* and *O. mykiss* as shown in the consensus tree (Fig. 5).

Sequence divergence estimates (Tables 4 and 5) were calculated separately for the genera *Salmo* and *Oncorhynchus* and the genera *Salvelinus, Salmo*, and *Hucho*: values varied from 0.66% for *S. malma* and *S. alpinus* to 5.74% for *S. namaycush* and *S. trutta* (Table 4) and from 0.98% for *O. kisutch* and *O. tshawytscha* to 5.07% for *O. kisutch* and *S. salar* (Table 5).

The phenograms obtained from the distance data using the Fitch–Margoliash and nearest neighbor methods differed only slightly from the trees obtained from the cladistic analysis of the data. The cladistic analysis of *Salvelinus* placed *S. namaycush* and *S. fontinalis* as sister species, while they were placed on adjacent branches in the phenograms obtained using the distance data. In the cladistic analysis of *Oncorhynchus* the position of *O. keta* was unresolved, but it was clustered with *O. nerka* and *O. gorbuscha* in the phenograms obtained using the distance data. The phenograms obtained from the data using the UPGMA method were very similar. The only differences were that *H. perryi* was clustered with *S. leucomaenis* and *S. confluentus* in the phenogram for the genus *Salvelinus* and that *O. masou* was clustered with

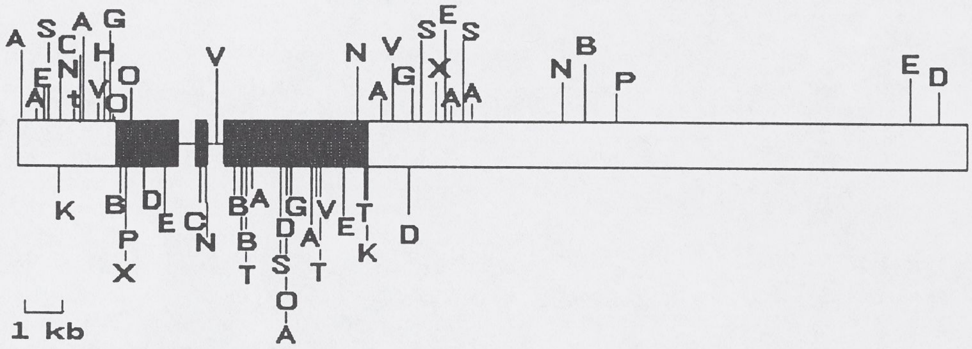

FIG. 2. Restriction map of the rDNA in salmonid fishes showing the sites which are conserved in all 17 species (below the line) and the variable sites which are present in at least two species (informative sites, above the line). Additional sites not shown which were found only in one species from left to right on the map include the following: 5′ETS: ApaI in *S. fontinalis*, HindIII in *S. namaycush*, ApaI and XhoI in *O. tshawytscha*, EcoRI in *O. kisutch*, KpnI in *S. confluentus*, and ApaI in *S. salar*; ITS: DraI in *S. fontinalis*; 28S: KpnI in *S. alpinus* and DraI in *S. malma*; IGS: PstI in *S. salar*, ApaI in *H. perryi*, NheI in *O. keta*, SspI and PvuII in *S. namaycush*, PstI and SstI in *S. trutta*, and BamHI in *S. leucomaenis*. There was also a HindIII site in the IGS just adjacent to the 28S in all of the species except *S. namaycush*.

TABLE 2. Summary of informative sites in the rDNA of salmonid fishes. These informative sites are shown above the map in Figure 2. They are listed in the order in which they appear on the map: sites 1–12 are in the 5′ ETS, site 13 is in the 18S, site 14 is in the ITS, site 15 is in the 28S, and sites 16–29 are in the IGS.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Hucho perryi	−	−	−	−	−	+	−	−	+	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
Salvelinus																													
S. namaycush	−	−	−	+	−	−	+	−	−	−	−	−	+	+	+	−	−	−	−	−	−	+	−	−	+	−	+	+	−
S. fontinalis	−	+	−	+	−	−	+	−	+	−	−	−	+	−	+	−	−	−	−	−	−	−	+	−	+	−	+	+	−
S. alpinus	−	−	−	+	−	+	+	+	−	−	−	−	+	+	+	−	−	−	−	−	−	+	+	−	−	−	+	−	−
S. malma	−	−	−	+	−	+	+	+	−	−	−	−	+	+	+	−	−	−	−	−	−	+	+	−	−	−	+	−	−
S. confluentus	−	−	−	+	−	+	−	−	−	−	−	−	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−
S. leucomaenis	−	+	−	+	−	+	−	−	+	+	+	−	+	+	+	−	−	−	−	−	−	−	−	−	−	−	−	+	−
Salmo																													
S. trutta	−	−	+	+	−	+	−	−	−	+	+	−	+	−	−	−	+	+	−	+	+	−	−	−	−	+	−	−	+
S. salar	−	−	−	+	−	+	−	−	−	+	+	−	+	−	−	+	+	+	−	+	+	−	−	−	−	+	−	−	+
Oncorhynchus																													
O. masou	−	−	−	+	−	−	−	−	−	−	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	+
O. mykiss	−	−	−	−	−	−	−	−	+	−	−	+	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	+
O. clarki	−	−	+	+	−	−	−	−	+	−	−	+	−	+	−	+	−	−	+	−	−	−	−	−	−	−	−	−	+
O. tshawytscha	+	−	+	+	+	+	−	+	−	−	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
O. kisutch	+	−	+	−	+	+	−	+	−	−	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
O. keta	+	−	−	+	+	−	−	−	−	−	−	+	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−	−	−
O. nerka	−	−	−	−	+	−	−	−	−	−	−	+	−	+	−	−	−	−	+	−	−	−	−	+	−	−	−	−	−
O. gorbuscha	+	−	−	+	+	−	−	−	−	−	−	+	−	+	−	−	−	−	+	−	−	−	−	+	−	−	−	−	−

TABLE 3. Summary of restriction sites in the rDNA of salmonid fishes.

Subregion	Conserved	Variable	Informative	Total	% informative
5′ETS	1	22	12	22	61
18S	6	1	1	7	14
5.8S	2	0	0	2	0
ITS-1, ITS-2	0	2	1	2	50
28S	15	3	1	18	6
IGS	1	25	14	27	50
Total	25	53	29	78[a]	38

[a]Includes one 0.5-kb insertion in the 5′ETS.

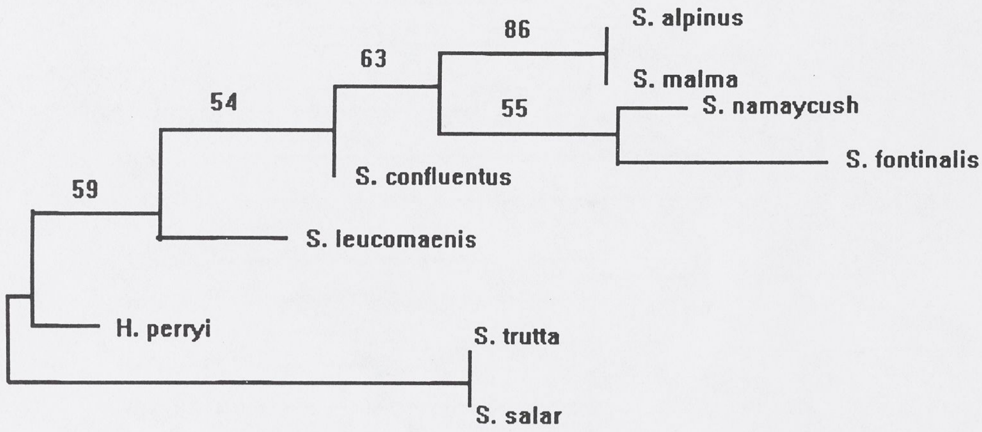

FIG. 3. Single minimum-length tree generated by the PAUP program with the informative sites in the rDNA for the six *Salvelinus* species and *H. perryi* with the two *Salmo* species as an outgroup. Numbers indicate bootstrap values.

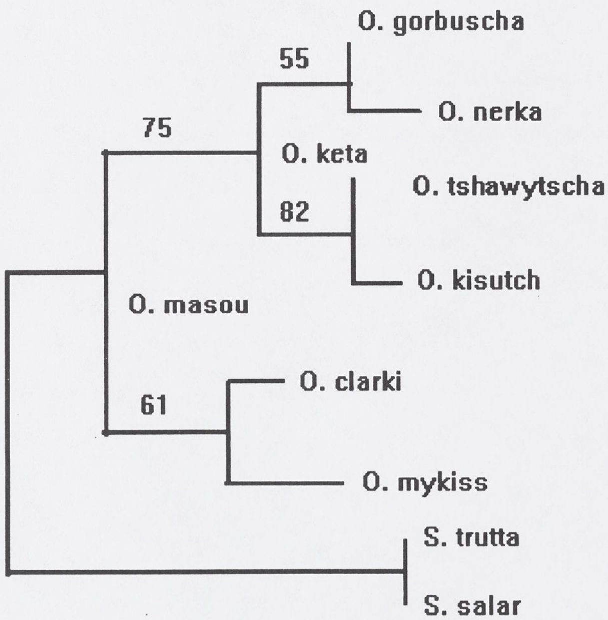

FIG. 4. Consensus tree generated by the PAUP program with the informative sites in the rDNA for the *Oncorhynchus* species with the two *Salmo* species as an outgroup. Numbers indicate bootstrap values.

O. clarki and *O. mykiss* in the phenogram for the genus *Oncorhynchus*.

Intraspecific Variation in *S. alpinus* and *S. malma*

Intraspecific differences in several restriction sites were found among various populations of *S. alpinus* and one difference was found between the various populations of *S. malma* (Table 6). For *S. alpinus*, the three European populations (*S. a. alpinus*) were identical, two populations from the high Arctic (*S. a. erythrinus*) were identical, and the two populations from southern Alaska (*S. a. ''taranetz''*) were identical at the sites examined. The two populations of *S. malma lordi* were also identical. When a cladistic analysis was done of the four subspecies of *S. alpinus* and the two subspecies of *S. malma* using *S. namaycush* and *S. fontinalis* as outgroups, 14 different trees were generated. Although *S. a. alpinus* and *S. a. oquassa* were always on the same branch, the other branches were unresolved with this data.

Discussion

Structure of Ribosomal DNA

The length of the repeating unit of the rDNA in salmonid fishes varies between 22 and 26 kb; most of the length variation occurs within each species (Phillips et al. 1989b; Phillips and Pleyte 1991). In fact, intraindividual variation in total length of the repeating units was very common. The variation in the total length occurs primarily in the IGS and is particularly noticeable in a region 3′ to the 28S coding region. The majority of restriction enzymes that cut in this region yield a set of closely spaced bands in each individual. Cloning and sequencing of this region in *S. namaycush* has shown that the length variation is the result of the insertion of variable numbers of a 89-bp repeat in the IGS adjacent to the 28S coding region in different copies of the rDNA within an individual (Zhuo 1991). Some length variation was also observed in the ETS region adjacent to the 18S coding region, but this variation was usually fixed in a given species. The lengths of the ITS-1 and ITS-2 were remarkably conserved in all of the species.

As expected from other studies of rDNA in vertebrates (reviewed in Gerbi 1985; Mindell and Honeycutt 1990) the 5.8S and 18S regions were the most highly conserved, then the 28S coding region, followed by the transcribed spacers, and the IGS. There were 25 sites which were conserved in all species and an additional 27 conserved in *Salvelinus* species. There were 28 conserved sites in *Oncorhynchus* species with one additional site also conserved in the Pacific salmon. A total of 37 sites were conserved in the two species of *Salmo*, providing additional evidence of the close relationship between these two species and the considerable genetic distance between them and the *Oncorhynchus* species.

The highest number of informative sites was found in the 5′ETS. Sites in the 5′ETS are particularly appropriate for the identification of species hybrids. We have shown (Phillips and Pleyte 1991) that F1 hybrids between *S. fontinalis* and *S. confluentus* had the banding patterns expected with the four enzymes which exhibit differences in this region in these two species.

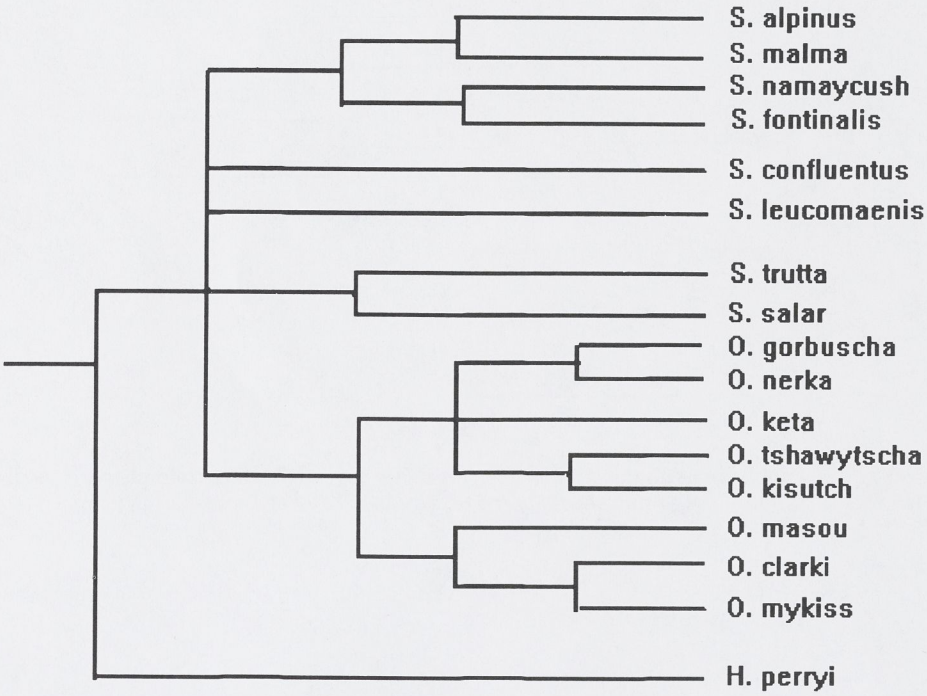

FIG. 5. Strict consensus tree obtained for the 17 species using the maximum parsimony method of the PAUP program and *H. perryi* as an outgroup.

TABLE 4. Matrix of percent sequence divergences (above diagonal) and numbers of shared restriction sites (below diagonal) among rDNA restriction maps for *H. perryi*, six *Salvelinus* species, and two *Salmo* species.

	Huc	leu	con	fon	nam	mal	alp	tru	sal
Huc	0.00	2.81	2.48	3.72	4.56	3.37	3.60	4.06	3.50
leu	30	0.00	2.02	2.64	3.94	3.39	3.61	4.04	4.04
con	28	31	0.00	2.89	3.13	2.02	2.26	3.83	3.83
fon	28	32	29	0.00	2.64	2.64	2.86	5.52	5.52
nam	27	30	29	32	0.00	2.35	2.57	5.74	5.74
mal	29	31	31	32	33	0.00	0.66	4.59	4.59
alp	29	31	31	32	33	37	0.00	4.80	4.79
tru	29	31	29	28	28	30	30	0.00	1.71
sal	30	31	29	28	28	30	30	37	0.00

TABLE 5. Matrix of percent sequence divergences (above diagonal) and numbers of shared restriction sites (below diagonal) among rDNA restriction maps for eight *Oncorhynchus* species and two *Salmo* species.

	tru	sal	clk	myk	mas	tsh	kis	ket	ner	gor
tru	0.00	1.71	3.72	3.83	3.83	3.94	4.50	4.65	4.79	4.65
sal	37	0.00	4.28	3.27	3.27	4.50	5.09	4.65	4.79	4.65
clk	30	29	0.00	1.04	1.59	1.78	2.89	2.40	1.90	1.84
myk	29	30	31	0.00	1.64	2.99	2.99	2.48	1.96	2.48
mas	29	30	30	29	0.00	2.40	2.99	1.90	1.96	1.90
tsh	30	29	31	28	29	0.00	0.98	1.54	2.15	1.54
kis	29	28	29	28	28	33	0.00	2.09	2.15	2.09
ket	28	28	29	28	29	31	30	0.00	1.64	1.04
ner	27	27	29	28	28	29	29	29	0.00	0.53
gor	28	28	30	28	29	31	30	31	31	0.00

Salvelinus Systematics

The major unresolved problems in the genus *Salvelinus* include the relationship of the Asian *S. leucomaenis* to the North American *Salvelinus* and the placement of the North American *S. confluentus* with respect to the other species. In addition the relationships among various populations and named subspecies of *S. alpinus* and *S. malma* in North America are also unclear.

Because *S. leucomaenis* was not included in previous allozyme and mtDNA surveys, the only published data concerning its relationships to other species have been from morphological

Table 6. Variable restriction sites in the rDNA of *S. alpinus* and *S. malma*.

Population	ApaI (ETS)	KpnI (28S)	SspI (IGS)	DraI (28S)	DraI (IGS)	*N*
S. alpinus,						
s. a. alpinus						
Storvaln, Norway	–	+	+	–	+	6
Lake Rannoch, Scotland	–	+	+	–	+	12
S. a. oquassa						
Bangor, ME	–	+	–	–	–	10
S. a. erythrinus						
Nayuk Lake, N.W.T.	+	–	–	–	–	10
S. a. ''tarentetz''						
Dolly Varden Lake, AK	–	–	–	–	–	10
East Finger Lake, AK	–	–	–			6
S. malma,						
S. m. lordi						
Auke Creek, Ak	+	–	–	+	–	4
Fox River (Kenai), AK	+	–	–	+	–	4
S. m. malma						
Noatak River, AK	–	–	–	+	–	4

comparisons (Behnke 1980; Cavender 1980; Stearley 1990) and karyological comparisons (Cavender 1984; Cavender and Kimura 1989; Phillips et al. 1989a, 1989b). Behnke (1980) suggested that *S. leucomaenis* was more closely related to *S. alpinus* and *S. malma* than to *S. namaycush* and *S. fontinalis* and placed these three species with *S. confluentus* in the subgenus *Salvelinus*. Both he and Cavender concluded that *S. leucomaenis* shares a number of characters with *S. confluentus* which is very similar to *S. albus* found in Kamchatcha. In two cladograms of species in the genus *Salvelinus* (Cavender and Kimura 1989), one based on morphological characters and the other on karyological characters, *S. namaycush* and *S. fontinalis* are on the first branch after *Hucho*, then *S. leucomaenis* and *S. confluentus* on a second branch, and finally *S. malma* and *S. alpinus*. However, Stearley's (1990) tree based on osteological data did not support this topology. The conclusion from the rDNA restriction site data is that *S. leucomaenis* is more closely related to *S. confluentus* than to the other *Salvelinus* species. This is also supported by a recent allozyme survey (Crane 1991) and by analysis of sequence data from a portion of the ITS-1 of the rDNA (Pleyte 1991).

It should be pointed out that the branching pattern of the species in the genus *Salvelinus* obtained from the rDNA restriction site data analysis is not congruent with distance data from both rDNA and mtDNA which suggest a close relationship between *S. confluentus* and *S. malma* and *S. alpinus*. There are several possible explanations for this. First, the branching pattern obtained from the rDNA data may not be correct, since the confidence limits are less than 90% as shown by the boostrapping results. Second, the branching pattern could be correct but the evolutionary rates might not be equal along the two branches. If the branch leading to *S. fontinalis* and *S. namaycush* is longer than the other branches, *S. confluentus* could be genetically closer to *S. malma* and *S. alpinus*, but still be lower on the cladogram than *S. fontinalis* and *S. namaycush*. Third, this could be the result of hybridization of *S. confluentus* with either *S. malma* or *S. alpinus* after the lineages had diverged. This might explain the closer genetic distance obtained between *S. confluentus* and the *S. malma* – *S. alpinus* complex with the mtDNA data, compared with the nuclear rDNA data. *Salvelinus confluentus* clustered within the *S. alpinus* subgroup in the tree based on mtDNA data. The number of informative sites obtained from both the rDNA and mtDNA restriction site maps was rather small, so that additional data from sequencing these molecules will be needed to resolve these relationships. Preliminary analysis of the sequence of part of the ITS-1 of the rDNA (Pleyte 1991) supported a close relationship between *S. confluentus* and *S. leucomaenis*, but the branching patterns among the six species were not completely resolved. We expect that complete sequencing of the ITS regions will yield sufficient data to resolve the relationships among the taxa in the genus *Salvelinus*.

Relationships among the various subspecies of *S. alpinus* and *S. malma* also remain controversial: Savvaitova (1980) suggested that they all belong to a single species. On the basis of morphology, Behnke (1984) suggested that there are three major groups of Arctic char with origins in Europe (*S. a. alpinus*), Siberia and the high Arctic region of North America (*S. a. erythrinus*), and a third form found in the Asian and North American drainages of the Chukotsk and Bering seas (*S. a. ''taranetz''*). The landlocked form in Maine (*S. a. oquassa*) is thought to be most closely related to the European form. Our data support Behnke's interpretation: each of these types has a different pattern of restriction sites, and the Maine form is most closely related to the European form (see Table 6). Behnke (1984) also assigned subspecific status to the northern and southern forms of *S. malma*. Both of these forms of *S. malma* were closest to the *S. a. erythrinus* subspecies of *S. alpinus*, but these groups were not well resolved with the limited data available.

Oncorhynchus Systematics

Problems also remain in the systematics of *Oncorhynchus*. The recent assignment of the Pacific trout with the Pacific salmon to the genus *Oncorhynchus* is based on many types of data (reviewed in Smith and Stearley 1989), and our results support this relationship. However, the relationships of the various Pacific trouts to each other and the Pacific salmon are still unclear. The trees based on rDNA data agree with those based on allozyme data (Utter et al. 1973) in placing *O. masou* close to the North American Pacific trouts (*O. mykiss* and *O. clarki*). The rDNA data did not support the tree obtained with mtDNA data in which these three species are clustered with *O. kisutch* and *O. tshawytscha* (Thomas et al. 1986; Ankenbrandt 1988). Questions also remain concerning the relationships among the three advanced Pacific salmon species. Trees based on allozyme and morphological traits place *O. gorbuscha* and *S. nerka* as sister species, while mtDNA and life history traits place *O. keta* and *O. gorbuscha* as sister species (reviewed in Smith and Stearley 1989). These two species also share a common t-RNA derived retroposon (Kido et al. 1991). The relationship between *O. keta* and the other two advanced Pacific salmon is unresolved by the rDNA restriction site data, but there was no support for a sister relationship between *O. keta* and *O. gorbuscha*. The congruence of data from morphology, allozymes, and nuclear rDNA on the one hand and life history and mtDNA on the other hand suggests that transfer of mtDNA following hybridization between diverged lines may have occurred. This possibility is also supported by the conflict between estimates of evolutionary divergence times between *O. keta* and *O. gorbuscha* of greater than 5–7 million yr based on fossil evidence (Smith et al. 1982) and estimates of divergence times of 1.25 million yr based on mtDNA divergence (Thomas et al. 1986). However, this assumes a rate of 2% substitution per million years per pair of lineages derived from mtDNA of mammals, and evidence is accumulating (Bentzen 1988) that rates are slower in teleosts. Only a few informative sites for these species were obtained in our analysis of rDNA, so that sequence data will be needed to help resolve the relationships between these species.

Our restriction site analysis has shown that the various spacer regions of the rDNA are evolving at rates appropriate for phylogenetic comparisons among species and genera of salmonid fishes. However, restriction site data have disadvantages for phylogenetic analysis. Site gains are more probable than site losses, and the accuracy of mapping is plus or minus 300 bp. The large size of the IGS, the numerous insertions found there, and the lack of a homologous probe to this region resulted in an incomplete mapping of this region. DNA sequence data would be the most desirable for phylogenetic analysis. The most informative sites were found in the 5′ETS. We are sequencing clones of this region from *S. namaycush* so that primers can be prepared for amplification and direct sequencing of the 5′ETS in different species. Regions of the rDNA which have interspecific variation, but very little intraspecific variation, would be the most desirable for sequencing. One such region is the ITS-1 which was used in a phylogenetic analysis of the great apes (Gonzales et al. 1990). We have designed primers for amplification of the ITS-1 and ITS-2 by the polymerase chain reaction and are in the process of accumulating sequence data on these regions that we hope will help resolve some of the unanswered questions in the systematics of this most interesting group of fishes.

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Jorge Dergam Dos Santos

Topic: STATISTICAL TREATMENT OF MOLECULAR DATA FOR PHYLOGENY RECONSTRUCTION

I) Introduction.

II) The character of DNA data.

1)Characters and characters states.

2)Alignment.

3)Parsimony.

4)Bootstrap analysis.

III) Literature.

I) INTRODUCTION

Molecular techniques have incorporated a new perspective for analyzing systematic problems, and have been succesfully applied in other areas. However, because of the nature of data, new challenges have been raised on the analysis of them.

Two competing schools of thought propose extremely different methods for analyzing and interpreting organic diversity: the pheneticists, and the cladists.

Pheneticists classify organisms based on overall similarity, while cladists consider that only shared derived (advanced) characters are informative for indicating the evolutionary relatedness among organisms.

Since pheneticists claim their analysis can be performed without any assumption (like the evolutionary process, speciation, and others), the outcome is that in morphological studies, different sexes may cluster in different groups if the species has sexual dimorphism, or young forms of different species may be grouped together (say, some caterpillars), while adults of their respective species are placed somewhere else. On the other hand, cladists make specific statement that the objective of their method is to find the best hypothesis to describe the evolutionary relationships among groups, and therefore their approach will be favored in this revision.

Phylogeny inference must be viewed as a "best guess" or "best estimate" of an evolutionary history based on incomplete information. The best phylogenetic tree (here used as a synonym of "cladogram") among a set of possible hypotheses is obtained by defining a specific sequence of steps (algorithm), or by defining a criterion that will allow us to choose the best tree among alternatives. The algorithm methods include phenetic methods such as the pair-group cluster analysis, which fail to addresss the underlying evolutionary assumptions, and we are left without the chance to rank suboptimal trees.

The second class has two steps: first, it defines the optimality criterion (the so-called objective function) for evaluating a given tree, and it is used when evaluating the tree against its alternatives. Second, it devises an algorithm for computing the objective function . This method generally assigns values for every tree, and thus alternative phylogenies can be ranked in order of preference (Swofford and Olsen, 1990).

Phylogenetic trees are composed of the following elements: contemporary taxa are the <u>terminal</u> <u>nodes</u>, or external nodes; the branch points within a tree are the <u>internal</u> <u>nodes</u>. The branches that connect (are incident to) pairs of nodes are also called links, segments or edges.

Trees may be rooted or unrooted; the first ones are the ones in which we are unable to determine the earliest point in time (no common ancestor specified), while the others have a hypothetical ancestor, typically by means of the inclusion of a group that lies beyond the limits of the target group.

II) THE NATURE OF DNA DATA.

Data generally fall within two major types: discrete characters and similarities or distances. Discrete characters are data about an individual species or sequence, while similarities or distances describe a pairwise relationship, or a quantitative comparison of two species or sequences.

Character data are preferred for phylogenetic analysis, since they allow the researcher to identify the informative value of specific portions of the sequences that may be rare or "signature" events (Farris, 1969).

DNA sequences may also be transformed to genetic distances, but that precludes the combined use of this information with other sets of characters (like morphological, behavioral, or chromosomal characters). Also, since data reported as distances cannot be transformed to their original form, part of the information is considered as lost in the transformation.

1) CHARACTER AND CHARACTER STATES

Character data are those for which a data matrix X assigns a character state x to each taxon i for each character j.

Characters are assumed to be independent, otherwise we would be forced to take covariances among studied characters, which would complicate the computational methods. Also, the independence assumption allows for a partition of each character in certain stages of computational algorithms. For example, numbers of substitutions can be minimized separately position-by-position and then summed over positions in a parsimony algorithm, or probabilities can be multiplied over positons in a maximum likelihood approach.

Character data may also be qualitative or quantitative. Qualitative ones may adopt two or more possible states. For example, for two states, they may be expressed as presence/absence, or 0/1.

When qualitative characters allow for more states, the change from one state to the other may be ordered (they are <u>allowed</u> to change in a specific direction), or unordered (there is no specific direction for change). The latter is the situation of nucleotide sequence data.

Along the sequence, the positions (offsets) correspond to "characters", and the "characters states" are represented by the nucleotide present in that position. For example, "position 83" may be the character, and "nucleotide C" is the character state.

The apparent straightforward analysis of molecular data presents an inherent difficulty: besides the requirement that analises must be performed on homologous molecules, it requires positional homologies for the sequences. Since this may only be obvious when checking very stable sequences, one must hypothesize insertion and deletion events that account for the gaps in the sequences under consideration.

2) ALIGNMENT

Sequence alignment is the most difficult component of phylogenetic analysis. Computerized alignment algorithms can align sequences using a "dynamic programming" like the Needleman-Wunsch method, which counts as 1 the matches (when the same element is present at corresponding position in both sequences), as zero when mismatches (positions containing different elements), and as negative score or penalties to gaps (positions at which part of one of the sequences is included in the gap).

Since any two sequences could be aligned perfectly if enough gaps were introduced, gaps must be penalized. The penalties may be a combination between size and number of gaps. Because there is no a priori reason for thinking that insertion/deletion events are more likely to involve short sequences, number of gaps are penalized more heavily than size of the gaps.

When sequences are compared to any other sequence in, say, a data bank, the extent of the degree of matching may be due to random similarity (there are only four bases that can occupy a given position in a sequence). Lipman and Pearson (1985) described a z statistic for that purpose, which is derived from the particular similarity score and the mean similarity score used in the search procedure. The z statistic equals the difference between the similarity score and the mean similarity score from the data base scan, divided by the similarity scores from the data base scan. They suggested the following headlines: z 3, possibly significant; z 6 probably significant; z 10, significant.

One of the approaches using pairwise alignment algorithms is the following:

taxon sequence

X	ATGCGAT
Y	ATCGAT
Z	ATGAT

one of the sequences is arbitrarily chosen as the "reference", then, each sequence is aligned to the referential sequence (here "X"). Whenever we have to add a gap to X, we do so with the other sequences too. The result will be:

taxon	sequence
X	ATGCGAT
Y	AT-CGAT
Z	AT--GAT

unfortunately, since the final alignment depends on the reference sequence, some authors make up T(T-1)/2 possible pairs for T sequences, they choose the ones that match the best, and one of them is taken as the reference

3) PARSIMONY

The most widely used numerical approaches to inferring phylogenies from character data are based on the principle of maximum parsimony, which essentially mantains that simpler hypotheses are preferable to more complicated ones and that ad hoc hypotheses should be rejected as much as possible. The underlying assumption for the explanation of attributes is that attributes common to groups of organisms are due to their inheritance from a common ancestor. Ad hoc hypotheses must be used, however, whenever conflict arises between characters, and in the phylogenetic framework, they are assumed as <u>homoplasies</u>, (convergence, parallelisms, or reversal); they are uninformative for phylogeny reconstruction.

Parsimony methods are applied to minimize total tree length of a phylogenetic tree, e.g.,the number of "steps" necessary to transform one character state in another.

In mathematical terms, maximum parsimony is described as the searching of all trees T such that

$$L(T) = E \quad E \quad w \ . \ \mathrm{diff}(x \quad , x \quad)$$

is minimal, where B is the number of branches, N is the number of characters, k and k are the two nodes incident to each branch k, x and x represent elements of the input data matrix or optimal character-state assignments made to internal nodes, and diff(y,z) is a function specifying the cost of a transformation from state y to state z along any branch. The coefficient w assigns a weight to each character; it is typically (but not necessarily) set to 1. Also, diff(y,z) need not equal diff(z,y), although for unrooted trees they have the same value.

Alignment procedures are usually subjected to maximum parsimony analysis, like PAUP 3.05 (Swofford, 1990), or by the use of dynamic weighting parsimony (Williams and Fitch, 1990).

4) BOOTSTRAP ANALYSIS

Once the phylogenetic tree is set up, bootstrap analysis (Efron, 1979, Felsenstein, 1985) is performed, in order to assess the nonrandomness of the tree. This method is a "resampling technique", and it operates by estimating the form of the sampling distribution by repeatedly resampling from the original data set. Data points are randomly sampled until a new data set containing the original number of observations is obtained. Under certain conditions (Efron, 1982), the distribution of the statistic of interest can be approximated from the distribution of the sample estimate over replications of the resampling process.

For constructing confidence intervals for phylogenies (Felsenstein, 1985), the amount of times that a particular group appears in each replicate sample (say, in 90% of them), it is used (from a frequentist point of view) to indicate that the group is supported at the 90% level. However, for the confidence limits to be valid, one must specify in advance the limits of the monophyletic group (derived from the most recent ancestor). Otherwise, we may be performing a multiple-test similar to the one used for comparing multiple means, with the consequent inflation of Type I error well above claimed rate. A second limitation of the bootstrap analysis is that it will be able to estimate variation if the data are in fact representative of the populational distribution. If this requirement is not met, then the confidence intervals are useless. A third limitation is that the number of characters must be "large" enough, although this aspect has not been yet worked out.

III) LITERATURE

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FW 501 Jorge A. Dergam

Topic: Comments on:

Grewe P.M., N. Billington, and P.D.N. Hebert. 1990. Phylogenetic relationships among members of Salvelinus inferred from mitochondrial DNA divergence. Can. J. Fish. Aquat. Sci. 47:984-991.

Recent trends for interpreting organic diversity for phylogeny reconstruction stress the need of attaining stability of classification by means of considering as many as possible sets of independent characters. While some researchers advocate for the congruence method (Shaffer et al., 1991), others support the total evidence approach, defined by Kluge (1989) as "the analysis of an unpartitioned body of data, ideally all of the data available for a group of terminal taxa".

As any partial approach, molecular systematics may (unwarrantedly) correctly evaluate molecular phylogenies instead of species phylogenies (Hillis and Moritz, 1991).

Reductionist techniques may lead to even more misleading conclusions about evolutionary relationships of taxa if the assumptions of their analysis are violated, and the methods used were devised to show mere degrees of overall similarity.

Specifically, weak points of the paper are:

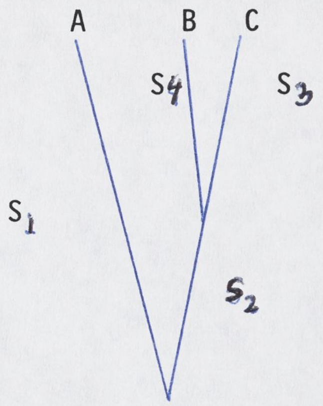
1) The title is partially misleading ("Phylogenetic..."), since one of the used methods is UPGMA (unweighted pair mean average), which is a phenetic approach. Phenetic approaches have as their only objective, the representation of the extent of the degree of similarity, and explicitly deny any concern about historical or genealogical branching order. Weaknesses of numerical methods are

enumerated and discussed in Mayr and Ashlock (1991)

Similarity or distance methods may give an accurate approximation of historical relationships, provided two conditions:

a) data must satisfy the three point property of ultrametricity. Ultrametric distances are described as:

For taxa A, B, and C, the distance between A and C (d_{AC}) is less or equal than the distances between A and B (d_{AB}), and between B and C (d_{BC}).



AC=2

AB=2

BC=1

AC<AB+BC

therefore, ultrametric data satisfy $S_1 = S_2 + S_4 = S_2 + S_3$. In other words, when we have three taxa, the two major distances must be equal.

Even satisfying this condition, the amount of divergence must be <u>linear</u> in time; in other words, we have to assume uniform divergence along time for all taxa and their mtDNA, a condition seldom if ever likely to happen (Hillis and Moritz, 1990).

c) sample sizes must be very large. Even in conditions where constant base substitution rates are real, small samples will present random fluctuations, again making it hard to represent real evolutionary relationships.

2) Swofford and Olsen (1990) point out that restriction endonuclease data violate the extremely basic assumption of character independence, and are

therefore unsuitable as input for phylogeny reconstruction. As exemplify by them, if one new site evolves (say, as a result of an insertion, deletion or a base substitution) between two older restriction sites, electrophoretic banding will reflect the change from one old large (longer) fragment being substituted by two shorter (lighter) ones. When two species are being compared, one with the primitive condition and the other with the derived one, the amount and size of the fragments of each of them will obscure the real homologies of the two (older) shared restriction sites.

3) Related to this fact, there are unequal probabilities for character state change: it is much easier to lo~~o~~se a restriction site than to gain a new one, and this property bears important implications for the validity of Wagner algorithm (see below).

4) Cluster analysis cannot join two taxa unless at least one pairwise distance links them (Swofford and Olsen, 1990). Thus, missing data within a group can force one or more members out of the group in the inferred tree. Although there are no missing data in the paper, the management of comparative data (instead of for example, character data, which would allow for the detection of meaningful data) is extremely dependent on the taxa included in the analysis, and therefore, sensitive to missing information. If this holds for mtDNA, let alone the missing information from other taxonomic sources of information.

5) Wagner parsimony was used for the arrangement of a Wagner tree. As we have seen, character state change is asymmetrical for gaining or lo~~o~~sing restriction sites, what it seems to be a violation of Wagner's parsimony assumption, which allows equal probability for change in any direction of character state.

6) Another source of error is related to the parsimony approach; parsimony

assumption works all right if changes at the level of analysis is small. Otherwise, long, unbranched lineages allow for multiple changes, which may in turn introduce an unknown degree of homoplasy (parallelism, convergence, and reversals).

7) Sensitivity to specific taxa in the tree. If trees represented real relationships, the arrangement would no be altered by pruning some of the taxa. Alternative trees, including Salvelinus leucomaenis (Behnke, 1989) resulted in different arrangements. Also, the exclusion of phylogenetically uninformative autapomorphies decreased the degree of parsimony, suggesting a high degree of arbitrariness of the proposed relationships.

It is easy to see that among all alternative methodologies that can be applied to a set of taxa, phenetic methods will be the most influenced by the nature of the data sets used for reconstructing the relationships among members of the taxa. This was acknowledged by Sokal (1985) "... phenetic techniques will not reach perfect congruence of classification, when these are based on different sets of characters". We would dare to say that the recognition of the same subgenera recognized by Behnke (1985) (Cristovomer, Baione, and Salvelinus) was more like a random event and not due to the weighting of the characters used.

As a conclusion, this paper goes nowhere, since:

a) it relies entirely on a small part of the genome (mtDNA), which has been shown to be able to "invade" the genome of related species and therefore provide erroneous data for phylogeny reconstruction. Pleyte et al. (1993) suggest the possibility of hybridization between the members of this genus; this will certainly make more difficult the interpretation of maternally-inherited characters like mtDNA. It would be wise to determine the correlation between this kind of data and the diploid kind of data

b) it transforms data characters in distances, a procedure that looses a certain amount of information (although it is difficult to assess how much is lost).

c) it applies a phenetic method (UPGMA), which objective is only to reflect degree of overall similarity, and an algorithm (Wagner tree), which gives one "best tree", without any other options (suboptimal trees).

The use of phenetical methods led Simpson (1964) to state that phenetics represents a "...retrogression in taxonomic principle... a conscoius revival of pre-evolutionary, eighteenth-century principles".

Alternative arrangements of the memmbers of the genus *Salvelinus* were based on morphology (Behnke, 1989), comparisons of nuclear organizer regions (references in Pleyte et al., 1993), restriction enzyme sites of ribosomal DNA (Phillips and Pleyte, 1991), and DNA sequencing of the first internal transcribed spacer (ITS1) of ribosomal DNA (Pleyte et al., 1993).

Benhke (1989) recognized three subgenera within the genus *Salvelinus*: *Cristivomer* with *S. namaycush*, *Baione*, with *S.fontinalis*, and *Salvelinus*, with *S. leucomaenis*, *S. alpinus*, *S. malma*, and *S. confluentus*.

As we have seen, Grewe et al. (1990) results corroborated the division of the three subgenera, but the relationships within subgenus *Salvelinus* were affected by the absence of *S. leucomaenis*.

On the other hand, Phillips et al. (1992), using mtDNA restriction map analysis of the 18S and 28S coding region, another species of *Hucho* as the outgroup, and cladistic as well as phenetic methods, concluded that *S.alpinus* and *S.malma*, and *S. namaycush* and *S.fontinalis* formed two separate species pairs. On the other hand, *S.confluentus* and *S. leucomaenis* did not pair so closely as the other ones. Bootstrap values, which estimate the nonrandomness of the cladogram branching were rather low:

59 for the branch leading to all the species of the genus, 54 for all of them setting S. leucomaenis aside; 63 for the branch joining the two pairs of species already mentioned; 86 for the pair S.alpinus/S. malma; and 55 for the pair S. namaycush/S. fontinalis. From the frequentist point of view, those values are interpreted as the proportional number of times that the true cladogram arrangement would be repeated over a large number of samplings.

However, Pleyte et al. (1993), working with DNA sequencing of one of the internal transcribed spacer regions (number 1), obtained bootstrap value of 100 for the branching of the genus in relation to Hucho, 100 for the pairing of S. confluentus and S. leucomaenis, 85 for the branching of the other two pairs, 98 for the pair S. alpinus/S. malma, and 92 for the pair S. fontinalis/S. namaycush.

These results are discussed in Pleyte et al. (1993), and will be briefly summarized here. Pairing S.leucomaenis and S.confluentus is supported by morphological similarity (Behnke, 1980) and also by allozyme study. These species also have deletions not present in the other species.

The division of the genus in three subgenera (Behnke, 1989) is not supported. not rejected The existence of three sister groups is supported by karyologycal data (Phillips et al., 1989)

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Evolutionary Relationships of the Salmonid Fish Genus *Salvelinus* Inferred from DNA Sequences of the First Internal Transcribed Spacer (ITS 1) of Ribosomal DNA

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DNA sequences of the ribosomal DNA (rDNA) first internal transcribed spacer region (ITS 1) of six species of the salmonid fish genus *Salvelinus (alpinus, malma, confluentus, leucomaenis, fontinalis,* and *namaycush)* and the closely related species *Hucho perryi* were determined. Phylogenetic analysis of the aligned sequences by both phenetic and cladistic methods with *H. perryi* as an outgroup generated one best topology which pairs *S. alpinus* with *S. malma* as the most recently derived species, and pairs *S. confluentus* with *S. leucomaenis.* Three other possible topologies favor the pairing of *S. namaycush* and *S. fontinalis,* with one tree placing them on separate branches, and vary the branching order of the interior groups. These results agree with previous studies based on comparisons of morphologies, isozymes, karyotypes, and restriction sites showing a close genetic relationship and possible hybridization between the members of this genus.

INTRODUCTION

Evolutionary relationships between the salmonid fishes of the genus *Salvelinus* have been studied by comparing morphologies, proteins, and karyotypes. Recent analyses comparing nucleolar organizer regions (NORs) (Phillips et al., 1989a,b) and restriction enzyme sites of ribosomal DNA (rDNA) (Phillips and Pleyte, 1991) and mitochondrial DNA (mtDNA) (Grewe *et al.,* 1990) have provided extensive new information, but relationships between some groups remain questionable. In this study, a phylogenetic tree for five North American and one Japanese *Salvelinus* species was produced by sequence analysis of the internal transcribed spacer region of the rDNA tandem repeat.

The three major tetraploid lines of North American salmonid fishes arose from polyploidization occurring about 50–100 million years ago (reviewed in Gold, 1979, and Allendorf and Thorgaard, 1984). They include the subfamilies Coregoninae (whitefish), Thymallinae (grayling), and Salmoninae (salmon and trout). The subfamily Salmoninae includes six genera: *Brachymystax, Hucho, Oncorhynchus, Salmo, Salmothymus,* and *Salvelinus*. The genus *Salvelinus* consists of five morphologically distinguishable species in North America: *S. alpinus* (Arctic char), which has a circumpolar distribution in the Arctic; *S. malma* (Dolly Varden char), found in sympatry with *S. alpinus* in the North Pacific; *S. confluentus* (bull trout), found in the Rocky Mountains; *S. namaycush* (lake trout) and *S. fontinalis* (brook trout), both of which are found widespread in North America. The only other major representative of the genus is *S. leucomaenis* (Iwana), which is found in the Far East (Behnke, 1989). Another Asian species, *S. albus,* formerly *S. kronicus* (Glubowsky and Cheresnev, 1981), has the same karyotype as *S. confluentus* and is believed to be closely related to it.

Behnke (1980, 1984, 1989) has divided the genus *Salvelinus* into three subgenera: *Cristovomer,* including *S. namaycush; Baione,* including *S. fontinalis;* and *Salvelinus,* including *S. alpinus, S. malma, S. cofluentus,* and *S. leucomaenis*. Savvaitova (1980) divides the genus into two groups: one of ancient origin, including *S. leucomaenis, S. fontinalis,* and *S. namaycush,* and the other originating about 10,000 years ago and including *S. alpinus* and *S. malma.*

The exact origin of the genus is unknown. Cavender (1980) has identified a 10-million-year-old fossil of *Salvelinus* from Nevada. Another fossil species, *Paleolox larsoni,* dating from the Miocene period (12–25 Mya), was found in Idaho (Smith *et al.,* 1982) and shares many features with *Hucho* and some with *Salvelinus.*

Studies of *Salvelinus* comparing morphologies (Behnke, 1980; Cavender, 1980; Stearley, 1990), isozymes (Clayton and Ihssen, 1980; Leary *et al.,* 1983), karyotypes (Cavender and Kimura, 1989; Phillips *et al.,* 1989a,b), and restriction site data (Grewe *et al.,* 1990; Phillips and Pleyte, 1991) have produced phylogenies with several different topologies. Most of these show a close relationship between *S. alpinus* and *S. malma,*

Sequence data from this article have been deposited in GenBank under Accession Nos. M94900–M94906.

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but the branching order of the other species varies. A study of mtDNA in *Salvelinus* using restriction map analysis (Grewe *et al.,* 1990) supports Behnke's hypothesis of three subgenera in finding a genetic distance of only 1.41–1.91 from *S. confluentus* to *S. alpinus* and *S. malma.* A sequence analysis of the mtDNA cytochrome b gene in *Salvelinus* (McVeigh and Davidson, personal communication) found a similar genetic distance of 0.35–1.03 between these species.

Although restriction map analysis of *Salvelinus* rDNA has provided further refinement of the phylogenetic relationships within the genus, questions still remain regarding the exact branching order of *S. confluentus, S. leucomaenis, S. fontinalis,* and *S. namaycush.* We chose to sequence a portion of the rDNA in these species to obtain further information.

Because rDNA has both rapidly and slowly evolving regions, it is particularly useful for phylogenetic analyses (Hillis and Davis, 1986; Hillis and Moritz, 1990; Mindell and Honeycutt, 1990). The slowly evolving conserved regions (coding regions) are useful in comparing distantly related species while the more rapidly evolving external transcribed spacer (ETS) and ITS regions are useful in comparing more closely related groups, such as species within a genus. A comparison of ITS 1 sequences was successfully used in a recent phylogenetic analysis of four species of primates (Gonzalez *et al.,* 1990).

The ITS 1 region of the rDNA tandem repeat was chosen as the ideal candidate for the comparison of species within the genus *Salvelinus* not only because of its intermediate rate of evolution, but also because it is particularly suited to the application of the polymerase chain reaction (PCR). Because the ITS 1 region is flanked by the highly conserved 18S and 5.8S genes, primers for its amplification can easily be designed from the known sequences of these genes in *Xenopus laevis,* mouse, rat, and primates. The ITS 1 region was also chosen for sequencing because it is about the same length in all salmonids (about 600 base pairs). In the present study the sequence data from seven species of *Salvelinus* were easy to align, allowing comparison by distance and maximum parsimony methods.

MATERIALS AND METHODS

Fish tissues for DNA extraction were obtained from the following sources: *S. leucomaenis* and *H. perryi* from Hokkaido Fish Hatchery, Japan; *S. namaycush,* Marquette stock, from Iron River Fish Hatchery, Michigan; *S. fontinalis* from Wisconsin Department of Natural Resources, St. Croix, Wisconsin; *S. confluentus* from Arrow Lake, British Columbia; *S. alpinus* from Nauyuk Lake, Northwest Territories; and *S. malma* from Auke Creek, Alaska.

DNA was isolated from liver by phenol extraction of proteins (Sambrook *et al.,* 1989).

The ITS 1 region of the rDNA was amplified from genomic DNA using the polymerase chain reaction (PCR). Primers for amplification (forward: 5′ AAAAAGCTTTTGTACACACCGCCCGTCGC 3′; reverse: 5′ AGCTTGCTGCGTTCTTCATCGA 3′) were designed from the 18S and 5.8S regions flanking the ITS 1, based on published sequences of these regions in *Xenopus laevis* (Salim and Maden, 1981) and *Oncorhynchus mykiss* (rainbow trout) (Nazar and Roy, 1978).

PCR reactions of 100-μl volume consisted of 1 μg of genomic DNA, 10 μl of 10× buffer (0.5 M KCl, 0.01 M Tris–Cl, pH 8.0, 0.1% gelatin, 0.015 M $MgCl_2$), and 350 pmol of each primer. Amplifications from DNA of *S. malma, S. alpinus,* and *Hucho perryi* required the addition of 1 Unit of Perfect Match (Stratagene) to eliminate the generation of extraneous products. Amplifications were carried out in a Coy Model 60 thermocycler (Coy Laboratory Products, Inc.) by 30 repetitions of a three-step cycle consisting of denaturation at 94°C for 1.5 min, annealing at 55° C for 2 min, and extension at 72°C for 3 min, and ending with a final extension at 72°C for 7 min. Products were purified by electroelution from agarose gels.

The double-stranded PCR products were sequenced directly or were blunt-end cloned into M13 for production of single-stranded sequencing templates. The Sanger (1977) dideoxy sequencing method was used in both cases.

The DNA sequences for the seven species were aligned by eye to yield a minimal number of evolutionary steps, with gaps inserted to maintain alignment. In areas of uncertain alignment, alternative alignments were tested. Informative sites were identified as those where at least two different character states are present, each represented in at least two of the species.

Percentage sequence divergences were determined by dividing the number of variable sites by the total number of sites. Genetic distances were determined by the Kimura two-parameter method (1980) using the DNADIST option of the PHYLIP program (Felsenstein, 1990). Trees were constructed from the genetic distances with the FITCH option of PHYLIP, which uses the Fitch–Margoliash (1967) method, and with the NEIGHBOR option, which includes the neighbor-joining method (Saitou and Nei, 1987) and the UPGMA method (Sokal and Michener, 1958).

Cladograms were constructed using two methods: Swofford's (1985) maximum parsimony program, PAUP, with the branch-and-bound option, using *H. perryi* as the outgroup; and the DNAPARS (maximum parsimony) option of PHYLIP, again with *H. perryi* as the outgroup. The four trees produced by PAUP analysis were input as User Trees and compared for significance with the DNAML option of the PHYLIP program. The PHYLIP DNABOOT program was used to generate a likelihood value for each branch from 100 random resamplings of the data, repeated 20 times.

RESULTS

The rDNA ITS 1 regions of six species of the genus *Salvelinus* and one species of the genus *Hucho* were sequenced (Fig. 1). The length of the ITS 1 in the aligned sequences was 596 base pairs with an average GC content of 63%. The seven species are 77% identical in sequence, while the six *Salvelinus* species share 82% identical sites. Of the 141 variable sites, 45 were phylogenetically informative, approximately 24% were transitions, 37% transversions, and 39% insertions or deletions. The transition to transversion ratio was approximately 0.64:1. Although a high number of transversions could result in increased homoplasy, a parsimony analysis considering only the transversion sites did not change the results.

Genetic distance values (Table 1) were determined using the Kimura (1980) two-parameter method and ranged from 0.53% between *S. alpinus* and *S. malma* to 9.49% between *S. fontinalis* and *H. perryi*. Differences between various species of *Salvelinus* and *Hucho* ranged from 7.01 to 9.49%. The greatest distances within *Salvelinus* were between *S. leucomaenis* and *S. fontinalis* (8.20%), and *S. fontinalis* and *S. confluentus* (7.63%). Percentage sequence divergences (Table 2) showed the same relative relationships between species.

The same tree was constructed from the genetic distance data using both the Fitch–Margoliash (1967) method and the neighbor-joining method (Saitou and Nei, 1987) of analysis (Fig. 2c). The tree groups the species into three sister pairs: *S. alpinus* with *S. malma, S. namaycush* with *S. fontinalis,* and *S. leucomaenis* with *S. confluentus,* with the first pair as the most advanced and the third pair closest to the outgroup. Analysis by the UPGMA (Sneath and Sokol, 1973) method differed by placing *S. namaycush* and *S. fontinalis* on separate branches (Fig. 2d).

Maximum parsimony analysis of the sequences with the PAUP program and with the DNAPARS program of the PHYLIP package using *H. perryi* as the outgroup generated the same tree as that from Fitch–Margoliash and neighbor-joining analyses of the distance data (Fig. 2c) and a second tree of equal length (114) which exchanges the placement of the two interior groups (Fig. 2b). Two other trees of longer length were also generated by PAUP: one, of length 115 (Fig. 2d), is the same as that generated by UPGMA; the other, of length 117 (Fig. 2a), maintains the pairing into three groups, but changes the branching order.

Bootstrap analysis of the sequences (Fig. 3) indicated a 98–100% occurrence of the branches pairing *S. alpinus* and *S. malma* and pairing *S. leucomaenis* and *S. confluentus,* and an 85–92% occurrence of the branch pairing *S. namaycush* and *S. fontinalis*. The branch pairing the sister groups together had the lowest occurrence at 68–85%.

Maximum likelihood analysis using the DNAML program of PHYLIP with the User Tree option was used to compare the four different trees (Fig. 2) which vary the arrangement of the interior groups. The ln likelihood values calculated for each tree were: Tree a, −1453.01562; Tree b, −1446.39270; Tree c, −1446.42139; Tree d, −1451.39429. Tree b is the best, but significance analysis (Kishino and Hasegawa, 1989) indicates the other three trees are not significantly worse.

DISCUSSION

ITS 1 Structure

In seven species of salmonids representing two genera, the aligned ITS 1 regions of the rDNA were found to be approximately 596 bp in length with 77% sequence similarity. The six species within the genus *Salvelinus* had 82% sequence similarity. A comparison of the ITS 1 regions of three species of Pacific salmon, *Oncorhynchus nerka* (sockeye salmon), *O. gorbuscha* (pink salmon), and *O. keta* (chum salmon) found a size of about 560 bp with 91–93% sequence similarity (M. Domanico, personal communication). Sizes of the ITS 1 among different organisms vary considerably, from 343 bp in the loach, 370–375 in herring and 567 in *X. laevis,* to 987 in gorilla, 1000 in mouse, and 1095 in human (Gonzalez *et al.,* 1990).

In addition to size difference, comparison of the *Salvelinus* ITS 1 sequences with those of yeast, frog, rat, mouse, loach (*Misgurnus fossilis*) (Kupriyanova and Timofeeva, 1988), and two herring species (*Clupea harengus* and *Clupea pallasi*) (Domanico, 1991) show virtually no sequence homology. The ITS 1 is believed to be a major site for the processing of the 45S pre-rRNA unprocessed transcript into the precursors for 18S and 28S + 5.8S rRNA (Hadjiolov *et al.,* 1984). Kupriyanova and Timofeeva (1988) found that in four vertebrates (loach, mouse, rat, and frog) the ITS 1 contained central complementary regions likely to form hairpin structures. In these species, areas corresponding to processing sites near the 18S and 5.8S genes were single-stranded and the 5′ end of the 18S rRNA was found to be complementary to a region close to one of these processing sites, suggesting that the ITS 1 secondary structure functions in forming the spatial geometry of the precursor molecule necessary for completion of the rRNA maturation process. Considerable variation in size and DNA sequence of the ITS 1 could be tolerated without hindering this function as long as a suitable arrangement of hairpin loops and juxtaposition of processing sites was maintained. This reduced level of constraint confers an intermediate level of evolutionary change on the ITS 1, making it appropriate for phylogenetic analysis of closely related species. Weighting variable sites within stems more heavily than those within loops of the proposed secondary

```
                                                     *
HUC ACGGGTTGCC AGCCGCCGGC ATGGGGCTGC GCTCCAGAAA CCAAACTCTG  50
LEU A......... .......... .........T .....GA... ...C.C....
CON A......... .......... .........T .....GA... ...A.C....
NAM A......... .......... .........T .....GA... ...A.C....
FON C......... .......... .........T .....GA... ...A.C....
MAL A......... .......... .........T .....GA... ...A.G....
ALP A......... .......... .........T .....GA... ...A.G....

           *
HUC CTGTGGTTG GGTTAGGGTA -GGGGGCTCC CGCCTCCCGC CTCTCCCTTC  100
LEU ...T...G.. ..-....... T........A ....--.C.. ...G...A..
CON ...C...T.. ..-....... T........A ....--.C.. ...G...A..
NAM ...T...T.. ..-....... T........A ....--.C.. ...G...A..
FON ...T...G.. ..-....... T........A ....--.T.. ...G...A..
MAL ...T...G.. ..-....... T........A ....--.C.. ...G...A..
ALP ...T...G.. ..-....... T........A ....--.C.. ...G...A..

                                        *        *
HUC TCTCGGCGCG GGTGTCTTTC GGTCTTAGCC CGG-TTGCCC CCGC-ATTCC  150
LEU .........G ......-C.. .......... ...G.---.. .T..T.....
CON .........G ......-C.. .......... ...G.T--.. .C..T.....
NAM .........A ......-C.. .......... ...-.T--.. .T..T.....
FON .........G ......-C.. .......... ...-.T--.. .T..T.....
MAL .........G ......-C.. .......... ...-.T--.. .C..T.....
ALP .........G ......-C.. .......... ...-.T--.. .C..T.....

            **        *
HUC TTTTGCCT-- GGGTTGCGCC CGACTGGCTC CATCCCCTTT CCCCGTTAGC  200
LEU ..TT....A- ....C..A.. ....C..... .......... ..........
CON ..TT....A- ....A..G.. ....C..... .......... ..........
NAM ..TT....-- ....T..G.. ....C..... .......... ..........
FON ..TT....-- ....T..T.. ....C..... .......... ..........
MAL ..AA....AA ....T..A.. ....C..... .......... ..........
ALP ..TT....AA ....T..A.. ....C..... .......... ..........

               * *
HUC CACGGCCACA TGACGCACCT ATGGGCGGGT GAGTCGGCCG CTACCGAAGG  250
LEU .......... T.G......T .....CA... .C......C. ..........
CON .......... C.G......T .....-A... .A......C. ..........
NAM .......... T.A......T .....CA... .A......T. ..........
FON .......... C.A......C .....CA... .A......C. ..........
MAL .......... T.G......T .....CA... .A......C. ..........
ALP .......... T.G......T .....CA... .A......C. ..........

                                            * *  **
HUC G-ACTGGGGG TGTCCGGTGA ACCGGGACTT CCCGAAATGG -TCTCACATT  300
LEU .-........ ....C..... .......C.. ...G...C.G -TCT.CC..T
CON .-........ ....C..... .......T.. ...G...C.G -TCT.CA..T
NAM .G........ ....C..... .......C.. ...G...T.G -TCT.CC..G
FON .-........ ....C..... .......C.. ...A...T.T TTTA.CC..T
MAL .-........ ....-..... .......C.. ...G...C.T -AAT.CC..T
ALP .-........ ....C..... .......C.. ...G...C.T -AAT.CC..T
```

FIG. 1. Aligned sequences of ITS 1 rDNA of *Hucho perryi* and six species of *Salvelinus*. Gaps are indicated by −; sites in common are indicated by .; informative sites are indicated by *. HUC, *H. perryi;* LEU, *Salvelinus leucomaenis;* CON, *S. confluentus;* NAM, *S. namaycush;* FON, *S. fontinalis;* MAL, *S. malma;* ALP, *S. alpinus.*

```
    ***      * *
HUC GTTAAAGCAG CTTGAGTATC GCCCAGTATC CTCGCGCGGC ACTGGGAACC  350
LEU GTG-T..CGT G....G.... .......... ..C..TT.G. C.C...A...
CON GTG-A..CGT G....G.... .......... ..C..TC.G. A.C...A...
NAM TTT-A..CGG C....G.... .......... ..C..TC.G. A.C...A...
FON TA--A..CGG C....A.... .......... ..T..TC.T. A.C...G...
MAL TAT-A..CGG C....G.... .......... ..C..TC.G. A.C...A...
ALP TAT-A..TGG C....G.... .......... ..C..TC.G. A.C...A...

                                                         *
HUC CAGTCAACCG CTCTGCGCCC CGGCCGAGGC GGGGGTTTAA TGTCTCCCC-  400
LEU .......... .......... ....CG.... .......... ......AC.-
CON .......... .......... ....CG.... .......... ......CC.-
NAM .......... .......... ....GC.... .......... ......CT.-
FON .......... .......... ....CG.... .......... ......CC.-
MAL .......... .......... ....CG.... .......... ......CC.C
ALP .......... .......... ....CG.... .......... ......CC.C

           *                 *
HUC AGCCCCCCCG GCGC--TTCG GCGA--GCGG CAGCG---GA GCACCCGGAG  450
LEU .....TAC.. .C..GC..C. ...TCG...C .G.C.GGA.. .........G
CON .....TCA.. .C..--..C. ...TCG...G .G.C.GGT.. .........G
NAM .....TCC.. .A..--..C. ...ACG...G .G.C.GGT.. .........T
FON .....TCC.. .C..--..G. ...ACG...G .G.T.GGT.. .........G
MAL .....TCA.. .C..--..C. ...ACG...G .G.C.GGT.. .........G
ALP .....TCA.. .C..--..C. ...ACG...G .G.C.GGT.. .........G

     * *     * **   *  *   *    * *   ***  *
HUC G-CCCCC--- -----TAATC TTAAACCAT- CTTGTCTTTG AACTATGGCC  500
LEU G-CAC..--A TTGTAA.AT. .T....C.TG .C--..A... ..........
CON TCAAC..CTA TT---A.AC. .T....C.TA .C--..A... ..........
NAM GGCCT..--- ------.TC. .G....A.GA .TTG..T... ..........
FON GGCAC..--- ------.AC. .G....A.GA .TTG..T... ..........
MAL G-CCC..--- ------.AC. .G....A.CA .TTG..-... ..........
ALP G-CCC..--- ------.AC. .G....A.CA .TTG..-... ..........

        *   *                                       *
HUC TCACGCTCTG GCGAAGGGCG GGCAGGGGGA AAGGAGGGCA ACCT-CCCAA  550
LEU ..T.A.T.T. GC....T... ...-.....A .......... ....-.....
CON ..T.A.T.T. GC....T... ...-.....A .......... ....-.....
NAM ..T.G.T.G. GC....T... ...-.....A .......... ....-.....
FON ..T.G.A.G. -A....T... ...-.....A .......... ....C.....
MAL ..T.A.T.T. GC....T... ...-.....- .......... ....C.....
ALP ..T.A.T.T. GC....T... ...-.....A .......... ....-.....

                                 *** ****
HUC CTCGGCCTAG CCACTAGCCT CTGCGTACAA CAGAAAAACA AGAGTA  596
LEU ...C.T.... .A........ ...T..A-AA AACA.AAA-. ......
CON ...C.T.... .A........ ...T..A-AA AAGA.----. ......
NAM ...C.T.... .A........ ...T..---- --G-.AAA-. ......
FON ...C.T.... .A........ ...T..A--- ----.AAA-. ......
MAL ...C.T.... .A........ ...T..ACAA CA--.AAAA. ......
ALP ...C.T.... .A........ ...T..ACAA C---.AAA-. ......
```

FIG. 1—*Continued*

structure could add further insight into the analysis, but a secondary structure has not yet been determined.

Comparison of Salvelinus *ITS 1 DNA Sequences*

Analysis of the ITS 1 DNA sequences by both distance and maximum parsimony methods generated the same best tree (Fig. 2b). Three alternate trees (Fig. 2a, 2c, and 2d) transposing the order of the interior groups were not significantly worse, but two of these (Figs. 2a and 2c) maintain the pairing of the species into three sister groups: *S. alpinus* with *S. malma, S. fontinalis* with *S. namaycush,* and *S. confluentus* with *S. leucomaenis*. The third (Fig. 2d) maintains two of the pairs, but puts *S. fontinalis* and *S. namaycush* on separate

TABLE 1

Matrix of Genetic Distance Values Generated from DNA Sequences of rDNA ITS 1 from Six *Salvelinus* Species and *Hucho perryi* Using the Kimura Two-Parameter Method

	alp	*mal*	*con*	*leu*	*fon*	*nam*
alp						
mal	0.53					
con	4.84	5.04				
leu	5.78	5.99	4.19			
fon	5.01	5.22	7.63	8.20		
nam	4.24	4.45	6.21	7.18	5.19	
Huc	7.37	7.78	8.21	8.98	9.49	7.01

Note: Names of taxa are abbreviated.

branches. Although the pairing of *S. fontinalis* and *S. namaycush* is favored, with an occurrence of 85–92% from bootstrap analysis, this arrangement was not statistically significant. Restriction site analysis of rDNA (Phillips and Pleyte, 1991) supports their position as a sister pair.

The trees generated by ITS 1 sequence comparison support both Behnke's (1980) and Cavender's (1980) observation of morphological similarities between *S. leucomaenis* and *S. confluentus,* but do not support Behnke's analysis (1980, 1984, 1989), dividing the genus into three subgenera. The pairing of *S. confluentus* with *S. leucomanis* is also supported by a recent comprehensive allozyme study (Crane, 1992). The placement of *S. confluentus* has varied in other studies, being paired with *S. namaycush* in Stearley's osteological comparison (1990), with a subspecies of *S. alpinus* in the mtDNA restriction site study of Grewe *et al.* (1990), and with *S. malma* in a recent analysis of mtDNA cytochrome b sequences (Davidson, personal communication).

The karyological data of Phillips *et al.* (1989a,b) agrees with the ITS 1 data in pairing the species into three sister groups. The tree generated from rDNA re-

TABLE 2

Matrix of Percentage Sequence Divergences among rDNA ITS 1 from Six *Salvelinus* Species and *Hucho perryi*

	alp	*mal*	*con*	*leu*	*fon*	*nam*
alp						
mal	1.34					
con	7.89	8.56				
leu	8.56	9.23	6.04			
fon	6.71	7.22	10.57	11.24		
nam	6.21	7.22	9.40	10.24	6.04	
Huc	10.57	11.07	12.42	12.92	13.09	10.91

Note: Names of taxa are abbreviated.

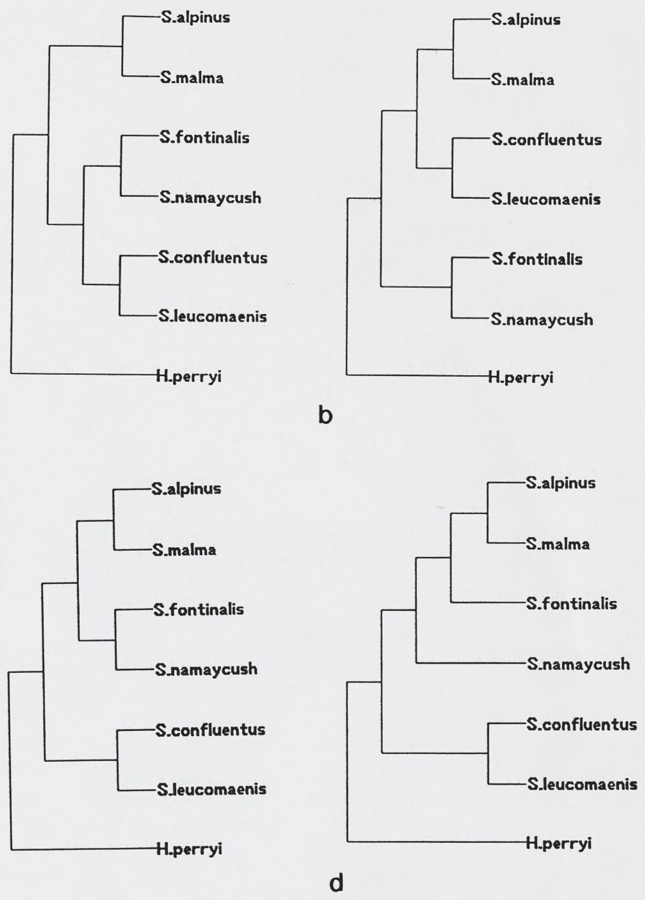

FIG. 2. Four different topologies for six *Salvelinus* species and *Hucho perryi* generated from analysis of rDNA ITS 1 sequence data. Tree lengths: a, 117; b, 114; c, 114; d, 115; ln likelihood values: a, −1453.01562; b, −1446.39270; c, −1446.42139; d, −1451.39429.

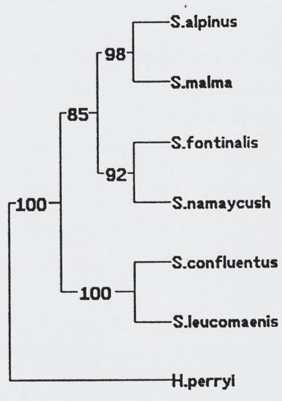

FIG. 3. Bootstrap analysis of consensus tree generated from rDNA ITS 1 sequence data of six *Salvelinus* species and *Hucho perryi.* Numbers indicate the number of times each branch occurred in 100 samplings of the sequence data.

striction site data (Phillips and Pleyte, 1991) supports the ITS 1 data in pairing *S. fontinalis* and *S. namaycush* as sisters and in the placement of that group closest to *S. alpinus* and *S. malma*.

In a noncoding region of DNA, without the benefit of codon constraints, correct alignment of sequences often cannot be determined with certainty. Especially in regions of multiple insertions or deletions, such as bp 451–470, 479–484, and 576–590 (Fig. 1), several reasonable alignments are possible. Of the 141 variable sites, 45 are phylogenetically informative, and of those, 25 are in areas of reasonably certain alignment. With the 20 sites in areas of uncertain alignment, alternative alignments were tested. Even though an occasional informative site was lost or introduced by these manipulations, the statistically significant portions of the original analysis remained intact.

Although the final result of our analysis is not dependent on these ambiguous regions, and they could be eliminated from the analysis, it is clear that regardless of exact alignment, *S. leucomaenis* and *S. confluentus* have insertions (bp 458–466) not present in any of the other species and *S. namaycush* and *S. fontinalis* have deletions (bp 577–584) not present in any of the others, both consistent with the pairings of species we found.

It is possible that some species and subspecies of *Salvelinus* have hybridized in the past, and this genetic mixing is complicating the elucidation of their phylogeny. The status of *S. alpinus* and *S. malma* have yet to be accurately assessed; Savvaitova (1980) believes they are the same species. The very small ITS 1 sequence divergence found between *S. alpinus* and *S. malma* in the present study suggests they are very closely related. Genetic distance estimates of mtDNA (Grewe *et al.,* 1990) and rDNA (Phillips and Pleyte, 1991) restriction site data also indicate that European and North American *S. alpinus* may have greater sequence divergence between them than that between North American *S. alpinus* and *S. malma*.

The position of *S. confluentus* in the phylogeny of *Salvelinus* varies among the different studies described. However, the similarity of the mtDNA of *S. confluentus* to *S. malma* and *S. alpinus* found by the restriction site analysis of Grewe *et al.* (1990) and by the sequence analysis of Davidson (personal communication) suggests the possibility of genetic contact between these species at some time. The distances based on the ITS 1 sequence data also showed that *S. confluentus* was closer to *S. alpinus* (4.84) and *S. malma* (5.04) than to any other species except *S. leucomaenis* (4.19). This is consistent with hybridization between a female *S. alpinus* or *S. malma* and males of *S. confluentus,* resulting in a mtDNA introgression with little or no nuclear gene flow across species, analogous to that observed in mice by Ferris *et al.* (1983). The inclusion in the analysis of additional subspecies, such as the Japanese *S. malma,* or the Asian species *S. albus,* which appears to have the same karyotype as *S. confluentus,* may be helpful. We are planning to examine additional DNA sequences from the ITS 2 and the ETS region to help resolve these species relationships.

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SMITHSONIAN INSTITUTION PRESS

Turtles of the United States and Canada

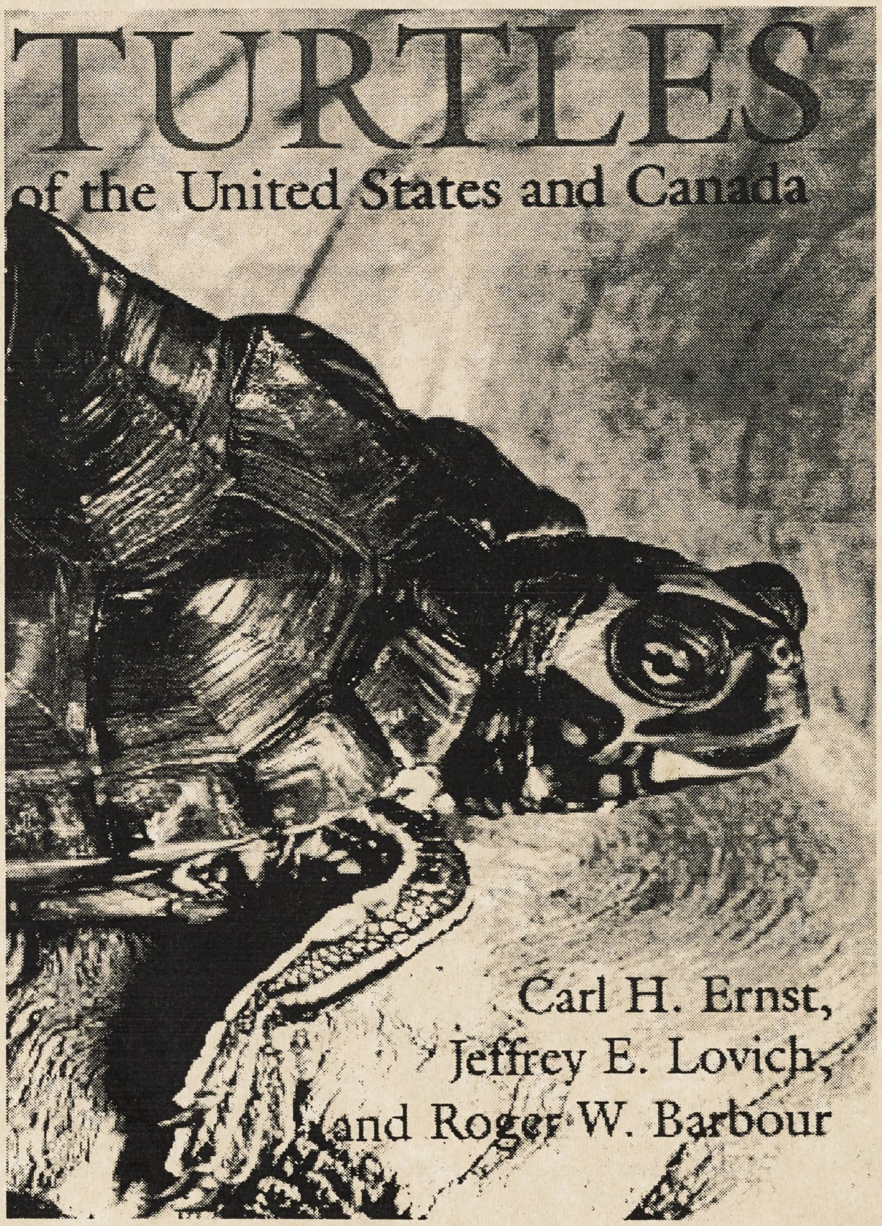
Carl H. Ernst, Jeffrey E. Lovich, and Roger W. Barbour

This fundamental reference book summarizes available knowledge about the turtle populations of the United States and Canada, representing the first comprehensive update in twenty years.

Since the original publication of *Turtles of the United States* in 1972, herpetologists have identified several new species of turtles indigenous to North America and doubled the information on the life histories and conservation of individual species. This book also incorporates new discoveries in biology, such as techniques in karyology, and the study of mitochondrial DNA relationships.

The book provides a survey of the fifty-six species in the United States and Canada—of which thirteen are protected under the Endangered Species Act. Each of the fifty-six species accounts includes sections on recognition, karyotype, fossil record, distribution, geographic variation, confusing species, habitat, behavior, reproduction, biology, growth and longevity, food habits, populations, and predators. The authors also include a discussion of turtle anatomy, a key to species identification, a pronunciation glossary for scientific names, and an extensive bibliography.

Illustrated with color plates and black-and-white photographs of each species, anatomical line drawings, and distribution maps, *Turtles of the United States and Canada* will be invaluable to herpetologists, wildlife and resource managers, biologists, and natural historians.



Carl H. Ernst, professor of biology at George Mason University, is the author of *Venomous Reptiles of North America* (1992) and coauthor with Roger W. Barbour of *Turtles of the World* (1989). **Jeffrey E. Lovich** is a wildlife biologist with the U.S. Department of the Interior's National Biological Survey in North Palm Springs, California. Before his death in 1993, **Roger W. Barbour** was professor emeritus at the University of Kentucky.

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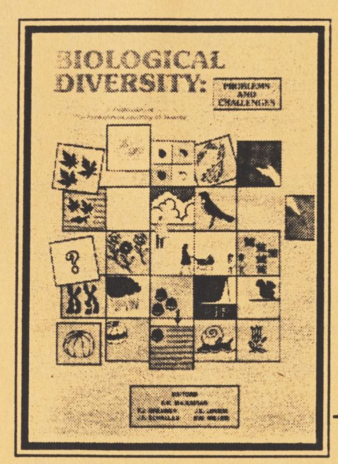

BIOLOGICAL DIVERSITY: PROBLEMS AND CHALLENGES

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PROBLEMS OF SYMPATRIC SPECIATION IN ICHTHYOLOGY

R. J. Behnke

Mayr, Linsey and Usinger define sympatric speciation as: "Speciation in the absence of geographic isolation." Formerly, many believed sympatric speciation to be an observed fact. Mayr has spoken forcefully against sympatric speciation and his influence on contemporary thought has resulted in the theory falling into disrepute.

The species flocks of cichlid fishes in Lake Nyassa, East Africa, of cottoid fishes in Lake Baikal, Siberia, and of cyprinoid fishes in Lake Lanao, Phillipines, are often advanced as arguments in favor of sympatric speciation. Brooks (1950) rejects Mayr's explanation of species flocks resulting from multiple colonization, but he also rejects sympatric speciation as the answer. Brook's intra-lacustrine isolation via geographic barriers would be acceptable to Mayr's point of view.

Many of the difficulties involved are semantic. In its simplest terms the question can be stated: Can a population of fish, or any sexually reproducing organism, enter a new environment and fraction off into distinct populations to utilize all niches of the environment, without benefit of geographic isolation? The problem is, how might isolating mechanisms be evolved as long as the population is in contact in a continuous environment?

Habitat preference and homing instinct might be the mechanisms of isolation for sympatric speciation in fishes, but they involve many unproved assumptions.

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THE COREGONID PROBLEM: A series of 8 papers by Gunnar Svardson, published in the Reports of the Institute of Freshwater Research, Drottingholm 1949 - 1957. Seminar presented by R. J. Behnke.

Svardson's work is an example of how recent advances made in various biological disciplines, mainly genetics, ecology and biostatistics can be applied to the ancient art of taxonomyin an attempt to solve a seemingly hopeless problem of classification. Svardson's oversimplification of his results and his disregard of traditional taxonomic tools such as comparative anatomy, opens him for criticism.

A multitude of whitefish species have been described from Europe. The perplexing number of varieties, often more than one from the same lake, challenged taxonomists for more than a century. Every detailed study, however, seemed only to add to the confusion. A widely held opinion prior to Svardson's work was that a single parent form of Coregonus was distributed around Europe in late Pleistocene times. From this single form a number of species arose in almost every drainage system it entered. Three ~~or~~ to four species occurring in a single lake such as Lake Constance were explained this way. Svardson, a strong foe of the concept of sympatric speciation, believes that 5 sibling species of whitefish and 2 sibling cisco species evolved in ancient pleistocene ice lakes in northern Europe and Siberia. From these centers of speciation the various species ranged over the continent and into North America. In some areas such as large, deep lakes with distinct niches, 2,3or 4 species can occur sympatrically without interbreeding. In other waters without such distinct niches, and without reproductive barriers to insure isolation, hybridization was encouraged, resulting in mixed populations and much trouble for the taxonomist.

Svardson's conclusions were based on the examination of thousands of specimens. Transplanting experiments in different environments revealed the variability and various phenotypic expressions of the characters used in whitefish taxonomy. The results led Svardson to reject all characters except gillrakers, which were not modified by the environment. Hybridization experiments proved that the various species were inter-fertile. Zoogeographic and geological evidence were used to hypothesize where and when speciation took place.

As Svardson points out, the clarification of such taxonomic problems could not be accomplished before the modern biological species concept was developed.

Fisheries Seminar

THE ROLE OF PLANTS AND BRUSH COVER IN FISH PRODUCTION
(Taken from Swingle, 1966)

		kg/ha	
		Shrimp	Bluegill
I.	UNFERTILIZED PONDS		
	A. Shrimp	45.4	-
	B. Shrimp with plants	236.7	-
	C. Bluegill	-	112.0
	D. Bluegill plus plants	-	140.7
	E. Bluegill, shrimp, plants	182.0	263.9
II.	FERTILIZED PONDS		
	A. Shrimp	637.7	-
	B. Bluegill plus shrimp	104.9	235.9
	C. Bluegill	-	154.3
	D. Bluegill, shrimp, brush	1173.5	236.8

III.	FERTILIZED PONDS	Cover	kg/ha
	A. Bluegill plus bass(300)	None	283.6
	B. Bluegill plus bass(300)	Yes	492.8
	C. Bluegill plus bass(600)	Yes	439.0

Uncertainty and Instream Flow Standards

By Daniel T. Castleberry, Joseph J. Cech Jr., Don C. Erman, David Hankin, Michael Healey, G. Mathias Kondolf, Marc Mangel, Michael Mohr, Peter B. Moyle, Jennifer Nielsen, Terence P. Speed, and John G. Williams

Several years ago, *Science* published an important essay (Ludwig et al. 1993) on the need to confront the scientific uncertainty associated with managing natural resources. The essay did not discuss instream flow standards explicitly, but its arguments apply. At an April 1995 workshop in Davis, California, all 12 participants agreed that currently no scientifically defensible method exists for defining the instream flows needed to protect particular species of fish or aquatic ecosystems (Williams, in press). We also agreed that acknowledging this fact is an essential step in dealing rationally and effectively with the problem.

Practical necessity and the protection of fishery resources require that new instream flow standards be established and that existing standards be revised. However, if standards cannot be defined scientifically, how can this be done? We join others in recommending the approach of *adaptive management*. Applied to instream flow standards, this approach involves at least three elements.

First, conservative (i.e., protective) interim standards should be set based on whatever information is available but with explicit recognition of its deficiencies. The standards should prescribe a reasonable annual hydrograph as well as minimum flows. Such standards should try to satisfy the objective of conserving the fishery resource, the first principle of adaptive management (Lee and Lawrence 1986).

Second, a monitoring program should be established and should be of adequate quality to permit the interim standards to serve as experiments. Active manipulation of flows, including temporary imposition of flows expected to be harmful, may be necessary for the same purpose. This element embodies the adaptive management principles that management programs should be experiments and that information should both motivate and result from management action. Often, it also will be necessary to fund ancillary scientific work to allow more robust interpretation of the monitoring results.

Third, an effective procedure must be established whereby the interim standards can be revised in light of new information. Interim commitments of water that are in practice irrevocable must be avoided.

The details of the monitoring program should vary from case to case. Where protection of particular populations is emphasized, the monitoring program should produce estimates of population size. However, population estimates by themselves often will not provide useful guides to action. This is particularly likely with anadromous fishes such as salmon, where populations of adults depend on harvest, ocean conditions, and other factors not related to instream flows, and populations of juveniles are hard to estimate accurately. Managers will learn more if the monitoring program also includes a suite of indices of the growth, condition, and development of the target species. These indices need to be interpreted with awareness of the complications arising from variations in life history patterns within and among populations. However, the indices and population estimates together will offer the best evidence of the mechanisms by which flows affect the survival and reproduction of individuals and thus the persistence of populations.

Daniel T. Castleberry is a fishery biologist with the U.S. Fish and Wildlife Service, Stockton, California. Joseph J. Cech Jr. and Don C. Erman are professors in the Department of Wildlife, Fish, and Conservation Biology, University of California-Davis. David Hankin is a professor in the Department of Fisheries, Humboldt State University, Arcata, California. Michael Healey is a professor at the Institute for Resource and Environmental Studies, University of British, Columbia, Vancouver. G. Mathias Kondolf is an associate professor of environmental planning, Department of Landscape Architecture, University of California-Berkeley. Marc Mangel is a professor with the Environmental Studies Board, University of California-Santa Cruz. Michael Mohr is a statistician for the National Marine Fisheries Service, Tiburon Laboratory, Tiburon, California. Peter B. Moyle is a professor in the Department of Wildlife, Fish, and Conservation Biology, University of California-Davis. Jennifer Nielsen is a research fisheries biologist for the U.S. Forest Service, Pacific South, and visiting scientist, Hopkins Marine Station, Department of Biology, Stanford University, Pacific Grove, California. Terence P. Speed is a professor in the Department of Statistics, University of California-Berkeley. John G. Williams is a consultant at 875 Linden Lane, Davis, CA 95616; jgwill@wheel.dcn.davis.ca.us.

The 1990 "Hodge Decision" in the case of *Environmental Defense Fund v East Bay Municipal Utility District* [Superior Court of Alameda County (California) No. 425955], with which several of us have been involved, exemplifies this approach. Judge Richard Hodge set flow standards for the American River, a major tributary to the Sacramento, that are intended to protect chinook salmon and other public trust resources from diversions by the East Bay Municipal Utility District. However, Hodge recognized the "fundamental inadequacy" of existing information regarding flow needs, so he retained jurisdiction and ordered parties to the litigation to cooperate in studies intended to clarify what the flow standards should be. Experience with these studies motivated the April 1995 workshop.

Our claim that there is now no scientifically defensible method for defining flow standards implies that the Physical Habitat Simulation Model (PHABSIM), the heart of the Instream Flow Incremental Methodology (IFIM), is not such a method. We have divergent views on PHABSIM. Some of us think that, with modification and careful use, it might produce useful information. Others think it should simply be abandoned. However, we agree that those who would use PHABSIM, or some modification of it, must take into account the following problems: (1) sampling and measurement problems associated with representing a river reach with selected transects and with the hydraulic and substrate data collected at the transects; (2) sampling and measurement problems associated with developing the suitability curves; and (3) problems with assigning biological meaning to weighted usable area (WUA), the statistic estimated by PHABSIM. Estimates of WUA should not be presented without confidence intervals, which can be developed by bootstrap methods (Efron and Tibshirani 1991; Williams 1996). Nor should any analytic method become a substitute for common sense, critical thinking about stream ecology, or careful evaluation of the consequences of flow modification, as has sometimes happened with the implementation of the IFIM.

Establishing instream flows involves both policy and science, and scientists and resource managers have challenging roles in the process. Managers need to accept the existing uncertainty regarding instream flow needs and make decisions that will both protect instream resources and allow development of knowledge that will reduce the uncertainty. Scientists need to develop and implement monitoring methods that will realize the potential of adaptive management, and develop the basic biological knowledge that will provide a more secure foundation for decisions that must balance instream and consumptive uses of water.

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Uncertainty and Instream Flow Standards: Perspectives Based on Hydropower Research and Assessment

By Webster Van Winkle, Charles C. Coutant, Henriette I. Jager, Jack S. Mattice, Donald J. Orth, Robert G. Otto, Steven F. Railsback, and Michael J. Sale

In a thought-provoking essay, "Uncertainty and Instream Flow Standards," Castleberry et al. (1996) argue that currently no scientifically defensible method exists [including the Physical Habitat Simulation System component (PHABSIM) of the Instream Flow Incremental Methodology (IFIM)] for defining instream flows needed to protect fish or aquatic ecosystems. They suggest (1) that an adaptive management approach is preferable, involving protective interim standards, a monitoring program, and an effective [institutional] procedure for revising interim standards in light of new information; and (2) that scientists and managers need to understand and consider the uncertainties in instream flow methods, develop and implement monitoring methods that will realize the potential of adaptive management, and develop the basic (mechanistic) biological knowledge about how flows affect the survival and reproduction of individuals.

We want to add to these constructive ideas to promote further discussion on the important issue of instream flow management. The scientific defensibility of any predictive assessment methodology needs to be judged based on its scientific foundations and its proven track record of use in specific environmental assessments. The adaptive management approach, while having a sound scientific foundation, is still developing a proven track record. Many perceive this approach as trial-and-error manipulations that provide an excuse for maintaining the status quo. Stated more strongly, adaptive management can be primarily a political process of adapting to changing political pressures, rather than a scientific process of adapting to increased scientific understanding. In reality, adaptive management requires dramatic experiments, including predictive models. We identify three additional needs to obtain the benefits of more flexible approaches such as adaptive management.

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Decision-making Framework

Adaptive management requires a high level of institutional, legal, and political flexibility—more than now typically occurs (Castleberry et al. 1996). Many fisheries agencies have insufficient resources for the current backlog of hydropower instream flow studies (Railsback et al. 1990), much less for long-term monitoring and adaptive management at each site. In addition, deregulation of electricity generation in the United States is creating a competitive climate such that hydropower operators will be less able to afford adaptive management experiments.

However, the benefits of flexible requirements are being recognized and gradually implemented. In addition to the "Hodge Decision" (Castleberry et al. 1996), examples include the settlement agreements for the Skagit River Project in Washington and the New Don Pedro Project in California, both of which allow flows to be varied according to agreed rules as more information and better models are obtained from monitoring studies. Additional opportunities for adaptive management lie with federal water projects [e.g., the Glen Canyon Project (U.S. Bureau of Reclamation 1995)]. Federal projects are not bound by the

> adaptive management can be primarily a political process of adapting to changing political pressures, rather than a scientific process of adapting to increased scientific understanding

procedures of the Federal Energy Regulatory Commission, and study and mitigation costs (including funding of resource agency participation) are heavily subsidized.

Management Objectives

A challenge to any approach based on population- or community-level effects is achieving agreement on management objectives that are acceptable to the public, simple to understand, ecologically meaningful, and measurable before designing a monitoring program or a model. The objective could range from target values for adult population density or production of a key fish species to maintainance of a balanced and indigenous fish community. Many of these objectives are difficult to measure. For example, providing a specified long-term average number of outmigrating salmon smolts per spawner may seem like a simple, well-defined management objective. However, determining whether this objective is being met based on variable and uncertain data gathered throughout the years is not simple. Nonetheless, the need to define such management objectives can be viewed as a strength of population- and community-level approaches (Orth 1995); while difficult, it does force decision makers to focus on real project effects, management options, and uncertainty.

Flow Manipulations, Monitoring Programs, and Models

The adaptive management approach requires several key components. The flow manipulation must involve a major change in the base flow regime for regulators and scientists to expect a measurable change. Minor flow changes may not provide the contrast needed to test the knowledge base and models used to develop management regulations and, thus, would fail to serve the decision-making purpose. While necessary for the adaptive management approach, flow manipulations and monitoring programs alone are not sufficient. For the adaptive management approach to be successful, it must include a methodology that provides two critical functions. First, it must provide the qualitative framework for identification and consensus-building concerning management objectives, flow manipulations, and monitoring. Second, it must provide a quantitative predictive tool [always combined with common sense, critical thinking about stream ecology, and careful evaluation of the actual consequences of flow modification (Castleberry et al. 1996)] that synthesizes the results from the monitoring program and makes quantitative predictions (absolute or relative) of fish population responses to alternative instream flow regimes and mitigation measures. Adaptive management can treat these predictions as hypotheses and design experiments to test their validity and improve predictions.

Although it has its weaknesses because of its limited focus on physical habitat, PHABSIM is such a tool. The individual-based modeling approach is another such tool that does not have this limitation. It replaces PHABSIM's reliance on habitat suitability curves with a mechanistic representation of the processes underlying fish growth, survival, and reproduction (e.g., Van Winkle et al. 1993). This representation varies with the life history of the species of interest, and density dependence (i.e., compensation) is an emergent population property of what happens to the individual model fish.

One such individual-based instream flow model (Van Winkle et al. 1996) is being developed in conjunction with a field evaluation of PHABSIM (Studley et al. 1996). By monitoring fish populations and habitat at 9 hydropower sites throughout 11 years and experimentally changing minimum flows (Studley et al. 1996), this study indicates that population responses to flow can be complex yet predictable. For example, at sites within one 5-km reach of the Tule River, California, factors that limited trout populations included base flows, scouring of redds by floods, winter temperatures too high for incubation, high summer temperatures, scarce spawning habitat, and interspecies competition. Physical habitat assessments alone cannot be expected to do well in such situations, yet many of these population-limiting factors have been successfully captured in the individual-based model and could be represented in a more comprehensive suite of models in IFIM. Preliminary results also indicate that relatively simple improvements to typical PHABSIM methods can produce instream flow assessments that are reasonably accurate and far less expensive than an adaptive management approach. At the very least, they can provide the initial predictions on which adaptive management can build.

Castleberry et al. (1996) correctly point out the uncertainties in simplistic instream flow assessments. We agree that the adaptive management approach has potential benefits and, in fact, we see a gradual trend toward more flexible assessment and management of water projects. However, before the adaptive management approach can be fully successful, it is clear that (1) decision-making frameworks; (2) management objectives; and (3) flow manipulations, monitoring programs, and models all need improvement. We emphasize that mechanistic models that depict the factors affecting the target aquatic resources (and not just physical habitat) must be key components of the adaptive management process. Without such models, the uncertainties may be greater than those currently encountered with habitat models, and as a consequence, eventual costs may be much higher than necessary.

Acknowledgments

The authors appreciate the constructive comments and perspectives of C. B. Stalnaker and two other reviewers. Preparation of this essay was supported by the Electric Power Research Institute under contract RP2932-2 (DOE ERD-87-672) with the U. S. Department of Energy, under contract DE-AC05-96OR22464 with Lockheed Martin Energy Research Corporation. This is Publication No. 4649 of the Environmental Sciences Division, Oak Ridge National Laboratory.

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...ssessment were followed in this

mussel should serve as a wake-up call to align the aquaculture interests in the United States. There is no question about it—the zebra mussel is here to stay. It can serve to either unify or shatter the industry—to make it viable and sustainable, or not. The choice is clear and is up to each American aquaculturist to ultimately make.

—*Rick Kastner*

Another look at instream flow standards

I read with interest the essay, "Uncertainty and Instream Flow Standards," in the August *Fisheries*. I must say that I was astounded that 12 people had to come together in that forum, similar to the 12 Apostles, to come to so obvious a conclusion. I have taken five or six 40-hour courses from the Fort Collins Instream Flow Incremental Methodology (IFIM) group since 1983, and I have used the methods. The IFIM training group stresses that the results of the IFIM should be used with caution and to supplement other information prepared for the decision-making process. I am a careful user of the method that provides various types of valuable information to help in the decision-making process. Let's not discard the method just because it does not give us "the answer." I did not see Bob Milhous, Ken Bovee, Terry Waddles, or others who are or were part of the IFIM training group in the forum (which could add considerable credibility) and perhaps could be a leader of the 12 to help clarify the appropriate uses of the IFIM.

The fact that they did come together in a forum suggests a question: Why did they have to come together? Probably because there was so much misunderstanding about the expections of the method. I hope this misunderstanding was an honest difference of opinion, but emotionalism and sophistry should not be ruled out in negotiations regarding use of water resources.

This leads to another question: How do we educate us all so that we can understand the limitations of the method? The educational process is embodied in critical thinking, intuitive reasoning, and the ability to understand how the IFIM works. So many entities take for granted that the results of the method are the end point of the analysis that will take a large effort of reeducation.

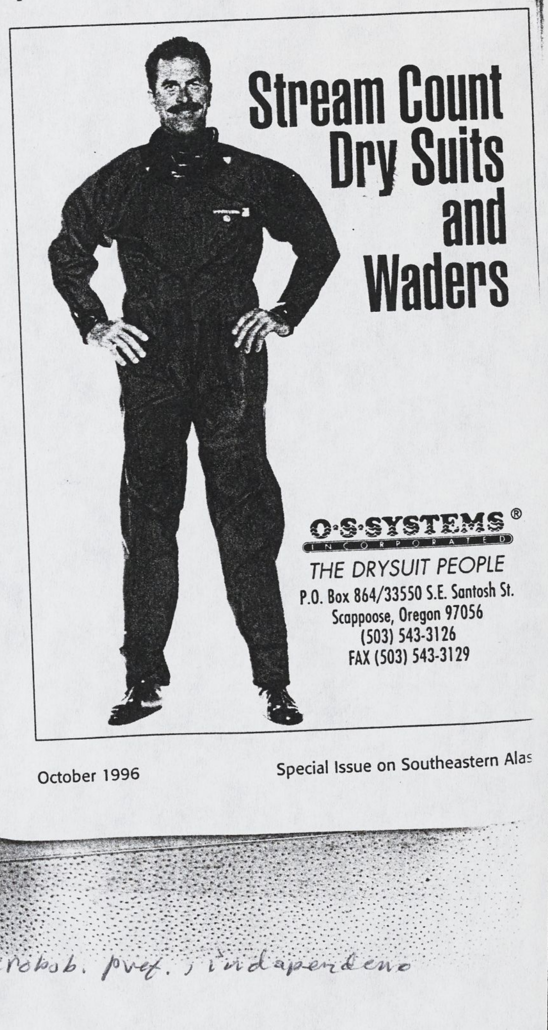
This begs the question: Who shall do the educating? Here the answer is perhaps obvious in a trilogy of sorts. The primary leaders will be the professors who teach the complex nature of ecological relationships and lead students to question and develop their reasoning ability. The secondary leaders will be the IFIM trainers. It is their duty to put into perspective how the results fit into the complex ecological environment and how difficult performing a limiting factor analysis consisting of more than three or four parameters in a complex ecosystem is. The tertiary leaders are the practitioners of the IFIM. They and they alone must make their clients and decision makers understand that the results of the IFIM are not the final answer. It is only one tool in combination with many others that will help to define the habitat or environmental conditions necessary for fish.

The results of the IFIM have been used as the final answer in a complex analysis of water resource issues. These issues have social, political, and even technical ramifications. As educated ecologists, we should know better than to take the results of any analysis that upon examination is simplistic and that obviously does not include room for the complexities. However, this is what has occurred when some practitioners of the IFIM have applied the method over the years. The IFIM uses basically three or four parameters in the development of weighted usable area. These are depth, substrate, and water velocity. Sometimes cover and other parameters are used. Based on common sense and the rigorous course in ecology that I took at Oklahoma State in the early 1960s (taught by Adolph Stebler) and the enlightening research methods at Oregon State in the late 1960s (taught by Charles Warren), I believe that there are more than three or four factors affecting distribution and abundance of fish, and it seems obvious that a species response is a result of a complex of environmental conditions, species interactions, human interference/harvest, and other factors.

—*Richard E. Craven*

Walleye-trout conflict airing appreciated

I want to thank the American Fisheries Society (AFS) for publishing the "Walleye and Northern Pike: Boost or Bane to Northwest Fisheries?" article by Thomas McMahon and David Bennett in your August 1996 issue of *Fisheries*. It is controversial, as noted, with some anglers supporting these species' introduction and a few taking it upon themselves to



TAFS 1997. 126(3): 536-42 - Microbiol. pref.; independence w/ flow

Transactions of the American Fisheries Society 126:536–537, 1997

COMMENTS

Comment: Testing the Independence of Microhabitat Preferences and Flow (Part 1)

Beecher et al. (1995) should be commended for trying to test one of the various assumptions of the physical habitat simulation model (PHABSIM). They noted Shirvell's (1990) report that juvenile steelhead *Oncorhynchus mykiss* used areas of stream with different water velocities at different flows, which suggested that the microhabitat preferences of juvenile steelhead can be a function of flow. Pert and Erman (1994) have found this true for adult rainbow trout, the nonanadromous form of *O. mykiss*. Because PHABSIM depends upon the assumption that microhabitat preferences are independent of flow, Beecher et al. recognized this as a serious problem and tried to test the assumption; however, their test is not persuasive.

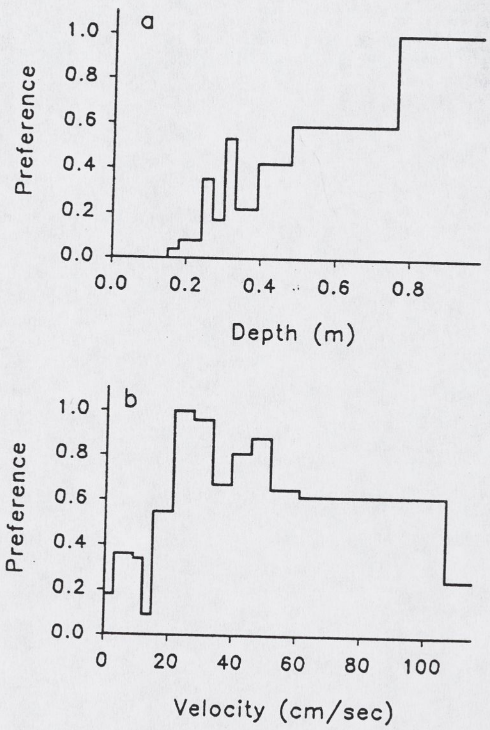


FIGURE 1.—Plots of depth preference (P[*d*]) and velocity preference (P[*v*]) for 104 steelhead parr (from Table 1 of Beecher et al. 1995).

In an earlier study, Beecher et al. (1993) developed preference criteria for depth and velocity from observations of 104 juvenile steelhead at a relatively low flow (Figure 1). In a later study, Beecher et al. (1995) measured depth and velocity at regular intervals along evenly spaced transects in an adjacent reach of the same stream at a relatively high flow. This gave them data at 242 points on a grid, which they took to represent an equal number of PHABSIM cells. (Each cell is centered on one of the grid points.) They also determined the positions of 21 juvenile steelhead, each of which was assigned to the depth–velocity cell nearest to the position.

To analyze the data from the later study, Beecher et al. (1995) used the product (denoted P[*dv*]) of depth preference (P[*d*]) and velocity preference (P[*v*]) for each cell. They divided the P[*dv*] range, which extends from 0.0 to 1.0, into four intervals such that approximately one-fourth of the cells fell into each range. Then they used the distribution of 21 fish among the four P[*dv*] intervals (Figure 2) to test "the hypothesis that depth and velocity preferences determined at one flow predict steelhead parr distribution at a different flow." Their null hypothesis was that fish would be distributed evenly over the four groups of cells. When this hypothesis was rejected by a chi-square test, they took this result as "validating the assumption of flow-independent preferences."

The logic of this claim is not apparent. The question is not whether juvenile steelhead distribute themselves evenly in streams regardless of depth and velocity, but whether their preferences for

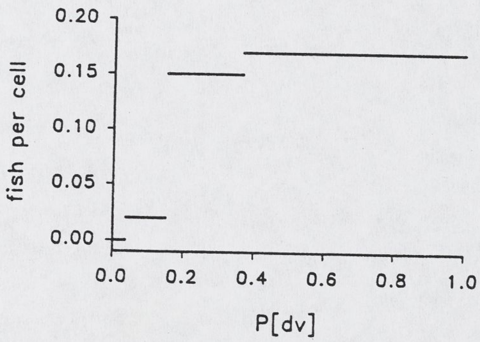


FIGURE 2.—Average numbers of steelhead parr (N = 21 fish total) observed per depth–velocity cell in four P[*dv*] intervals (horizontal lines; from Table 2 of Beecher et al. 1995).

depth or velocity change with flow. Should we believe that the depths and velocities at which the 104 and 21 steelhead parr were observed are samples from the same distributions? To answer this requires a different null hypothesis than the one used and probably a larger sample size. In any event, any number of sets of preferences for depth and velocity could give rise to given values of P[*dv*]—or to the observed frequencies (Figure 2), which are flat over a considerable range of P[*dv*]—so analyzing the data in terms of P[*dv*] does not seem helpful. Finally, it seems hard to assign biological meaning to the city-skyline shapes of the preference curves.

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Transactions of the American Fisheries Society 126:537–540, 1997

Comment: Testing the Independence of Microhabitat Preferences and Flow (Part 2)

Beecher et al. (1995) claimed to have validated an assumption of the instream flow incremental methodology (IFIM) and of its physical habitat simulation model (PHABSIM) that water depths and velocities preferred by fish are independent of streamflow. We disagree. First, the study compared habitat preference (of young steelhead *Oncorhynchus mykiss*) at low flow with habitat use (not preference) at high flow. Second, the statistical approach used can lead to the conclusion that depth and velocity preferences are the same at two flows even when most scientists would consider them different. Here, we address statistical issues that arise when comparisons of habitat distribution are based on fish preferences rather than on depth and velocity, and we recommend new techniques for comparing distributions.

Beecher et al. (1995) addressed the null hypothesis "fish distribution is independent of depth and velocity preferences determined at a different flow." They rejected the hypothesis on the basis of a goodness-of-fit test that compared the observed distribution of fish among preference quartiles at a high flow with the expected uniform distribution that would result if fish selected habitat without regard to preferences derived at a lower flow. (The test statistic was P[*dv*], the product of preferred depth P[*d*] and preferred velocity P[*v*].) We do not believe that rejecting this hypothesis implies similarity in fish preferences over a range of flows.

The comparison was of low-flow preference with high-flow *use*; the question of whether preference changed with flow should have been addressed by calculating preference at both flows. It can be shown mathematically that both habitat use and habitat preference cannot be flow-invariant. Habitat use must change in response to flow (i.e., to habitat availability). The original question remains, because preference might be flow-invariant though habitat use may shift.

Unlike traditional comparisons of habitat preferences in which univariate depth and velocity preference distributions are compared between two fish populations, Beecher et al. used preference ranges instead of depth–velocity ranges. Their frequencies were numbers of fish, but expected fish numbers were calculated with the number of P[*dv*] cells in each of four preference ranges: (expected number of fish) = (fraction of cells in preference range) × (total number of fish). This approach is unlikely to detect shifts in habitat preference because it compares the numbers of fish in each of four preference ranges (quartiles) between two flows. Collapsing data into ranges masks differences in depth and velocity preferences because many depth–velocity combinations can share the same P[*dv*] value. Consider a unimodal depth preference curve for trout at low flow. Intermediate depths are optimal, and both shallow and deep habitats are marginal. As flow increases, fish that had been forced to occupy shallow water may shift to deep water, as they did in Pert and Erman's (1994) study. If the fish distribution data are aggregated within preference ranges, shallow and deep fish would be lumped together in the low-preference category, and their joint proportion of the population might not change between low and high flows. In such a case, the test used by Beecher et al. would not detect the marked habitat shift that fish underwent. The same problem can arise with velocity, and the marginal preference range becomes an even greater catchall when both habitat factors are combined. Whether habitat is unsuitable because depth or another factor is too great or too slight is immaterial for IFIM calculations of weighted usable area (WUA) and instream flows. It does matter for testing and comparing preferences. Having the same proportions of fish in habitat deemed unsuitable, marginal, and optimal at different flows does not imply that the same depths and velocities were preferred.

The test used by Beecher et al. also had low power because their hypothesis was that high-flow use (assume it was preference) is independent of low-flow preference, rather than that preferences at the two flows are equal. The type I error rate is low for the hypothesis tested, and only large differences in preference would be diagnosed as real.

Thomas and Bovee (1993) used a test like that of Beecher et al. to evaluate transferability of IFIM habitat suitability curves. They quantified the relationship between type I and type II error rates and the number of occupied and unoccupied P[*dv*] cells. This test is strongly influenced by habitat availability because it depends on cell frequencies instead of fish frequencies. Its dependence on the quantity and characteristics of unoccupied cells is undesirable, because it seems unreasonable that a difference in preference between two flows should depend on the index values assigned to empty cells. Fish density may influence the degree to which "suitable" cells are occupied.

We suggest alternative tests that can detect smaller differences between preferences than the one used by Beecher et al. (1995), and we propose a way to define ecologically significant differences. As an illustrative example, we use the frequency distributions of preference for depth and velocity shown by adult rainbow trout (nonanadromous *O. mykiss*) at low and high flows (Pert and Erman 1994). Preferences shifted to deeper and faster water when flow increased (Figure 3). We chose this example because most people can agree without statistical confirmation that a clear shift in habitat preference occurred.

In two tests, we evaluated the habitat shift by resampling the joint depth–velocity preference distribution. Resampling provides confidence bounds of statistics with unknown distributional characteristics, such as the preference index. In our proposed tests and in an application of the Beecher et al. test, we used the true bivariate or joint preferences (P[*d,v*]) rather than the usual index (P[*dv*] = P[*d*] × P[*v*]).

In our first test, we resampled the habitat use data for each flow, drawing fish observed in different depth–velocity combinations. For each of 50 replicate samples, we calculated the differences between preferences at high and low flows. The 1% and 99% confidence bounds for several depth and velocity classes did not include zero (zero implies no difference between flows; Table 1). According to this test, preferences were significantly different at the two flows, particularly in deeper habitat.

In the second test, we focused on defining an ecologically meaningful statistic to describe the preference distributions. The peak of the WUA curve would be a good ultimate endpoint, but we chose the peak of the joint preference distribution P[*d,v*] as a simpler surrogate. We tested the hypothesis that the P[*d,v*] peak did not shift in response to flow. For all the low-flow samples we drew, the peak occurred within the depth range of 96–120 cm and the velocity range of 15–30 cm/s. At the high flow, 36% of the samples peaked within these ranges, but 64% peaked in deeper (120–144 cm) and faster (30–60 cm/s) habitat. A binomial test rejected the hypothesis that the peaks were the same at both flows ($|z| = 3.75$; $P < 0.0001$).

Finally, we applied the goodness-of-fit test used by Beecher et al. to the joint preference data organized in the following form:

Low-flow preference range	High-flow percentages of: Expected cells	Observed fish
0.0–0.1	54	40
0.1–0.3	22	26
0.3–1.0	24	34

The null hypothesis of independence from low-flow preferences was rejected ($\chi^2 = 8.46$; df = 2; $P = 0.014$).

These results appear to contradict one another. Although trout did not select habitat without re-

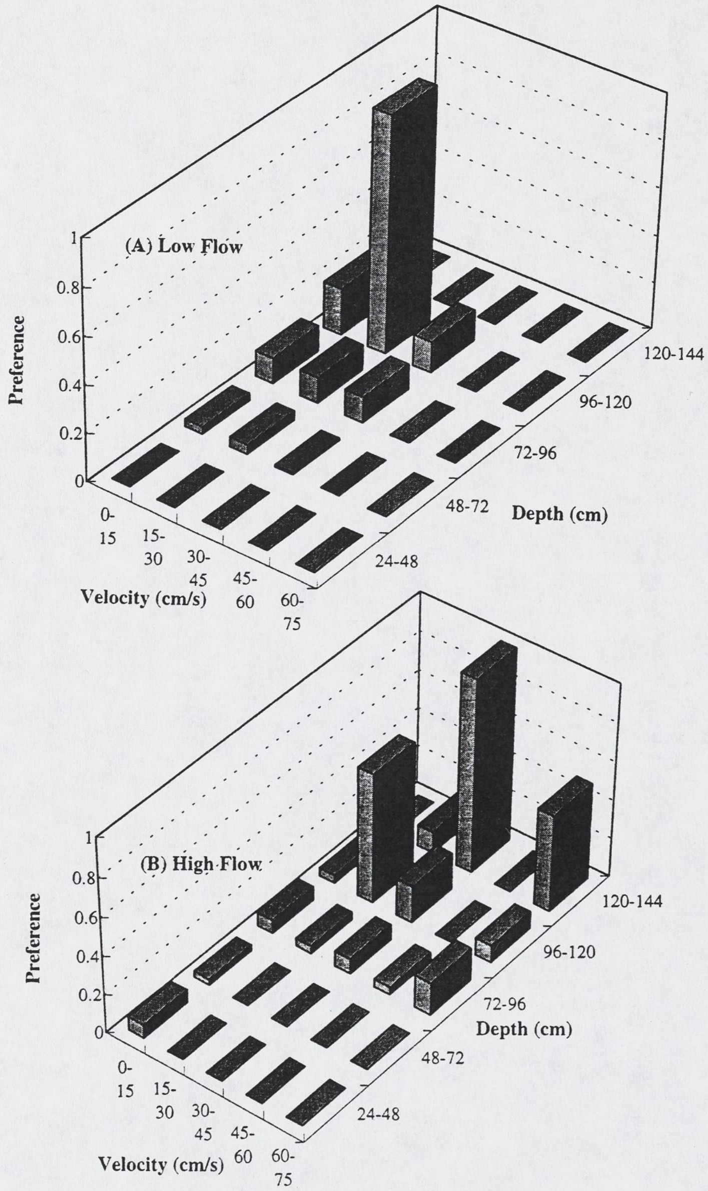

FIGURE 3.—Adult trout preferences calculated as a function of river depth and velocity for (A) a low flow and (B) a high flow.

gard to low-flow P[*d,v*], their habitat preferences shifted to greater depths and velocities with increased flow. This contradiction is possible because the tests are mirror images of one another and because the probability of a type I error (reject when true) is set to a low value ($\alpha \leq 0.10$) for each. Fish in these samples fell into the wide intermediate area between extremes of complete and no constancy in habitat preference with changes in flow. Which test is better, and which level of type I error is acceptable? Ecologists are coming to realize that the balance between type I and type II errors should be reasonable in terms of ecological significance (Quinn and Dunham 1983; Roughgarden 1983; Toft and Shea 1983). In our case, it is misleading to use a test that rejects the null hypothesis at the slightest similarity and then claim that no shift in preference has occurred.

TABLE 1.—Resampling test of the hypothesis of zero difference between high-flow and low-flow joint preferences of rainbow trout for depth and velocity. Values are the sample differences in preference (high flow minus low flow) and (in parentheses) the nonparametric 1% and 99% confidence bounds determined by resampling. Asterisks indicate significant differences from zero ($P \leq 0.01$; i.e., 98% of the range of simulated differences failed to bracket zero). Parenthetic words in place of confidence bounds mean that a habitat combination was present only at low flow (low), at high flow (high), or at neither flow (neither).

Depth class (cm)	Velocity class (cm/s)				
	0–15	15–30	30–45	45–60	60–75
0–24	0.00 (0.00, 0.00)	(neither)	(neither)	0.00 (low)	0.00 (low)
24–48	0.07 (0.00, 0.18)	0.00 (high)	0.00 (0.00, 0.00)	0.00 (low)	(neither)
48–72	0.01 (−0.08, 0.08)	−0.04 (−0.14, 0.00)	0.00 (0.00, 0.00)	0.00 (0.00, 0.00)	0.00 (high)
72–96	−0.04 (−0.27, 0.18)	−0.07 (−0.22, 0.01)	−0.03 (−0.28, 0.10)	0.09 (0.10, 0.54)*	0.04 (0.00, 0.19)
96–120	−0.16 (−0.56, −0.03)*	−0.34 (−0.77, 0.00)	0.09 (0.04, 0.80)*	0.08 (0.00, 0.26)	0.00 (0.00, 0.00)
120–144	(neither)	0.11 (high)	0.95 (0.55, 1.00)*	0.50 (high)	(neither)

However, small shifts in preference that do not influence the predicted relationship between WUA and streamflow may be tolerable.

How do we detect differences that are ecologically significant? One good way is to determine the magnitude of shift in depth or velocity preference that would significantly change peak WUA. Williams (1996) showed that variation in preference curves can cause large differences in peak WUA. Once the magnitude of a significant preference shift has been defined, one can design habitat studies with adequate power for detecting such a shift. If a compilation of IFIM studies allowed flow-related changes in habitat availability to be characterized, general guidelines might be developed that would circumvent the need for a new IFIM study on every regulated stream.

In summary, we recommend the following protocol for comparing habitat preferences. (1) Conduct comparisons with regard to bivariate depth and velocity distributions, not with regard to preferences. (2) Use resampling methods to obtain confidence bounds on indexes (such as preference) with unknown distributional properties. (3) Define a magnitude of preference change that is ecologically significant in terms of its effect on the predicted WUA–streamflow relationship.

Acknowledgments.—We received helpful reviews from Steven Railsback, Hal Cardwell, and John Beauchamp. Ken Rose suggested the resampling test. Oak Ridge National Laboratory is managed by the Lockheed Martin Energy Research Corp. for the U.S. Department of Energy under contract DE-AC05-96OR22464. This is publication 4678 of the Environmental Sciences Division.

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Transactions of the American Fisheries Society 126:541–542, 1997

Testing the Independence of Microhabitat Preferences and Flow: Response to Comments

Williams (1997, this issue) and Jager and Pert (1997, this issue) suggest we incorrectly concluded (in Beecher et al. 1995) that depth and velocity preferences (P[*d*] and P[*v*]) of juvenile (parr) steelhead *Oncorhynchus mykiss* do not change with flow. We originally estimated steelhead preferences at low streamflow (Beecher et al. 1993). When we tested the estimates at substantially higher flow, steelhead parr occurred most frequently in areas giving high combined depth–velocity preference values (P[*dv*] = P[*d*] × P[*v*]). Williams and Jager and Pert believe our test was inconclusive because similar values of P[*dv*] can result from several combinations of P[*d*] and P[*v*] and thus can mask flow-related changes in depth and velocity preferences that might have occurred. Nevertheless, we think our results are consistent with our conclusion that depth and velocity preferences determined at one flow predict fish distribution at a different flow.

We did not directly compare depth and velocity preferences at low and high streamflows, as Williams and Jager and Pert urge, but we did recognize from Shirvell's (1990) study that both utilization and preference cannot remain unchanged at different flows. The question that concerned us was: Do depth and velocity preferences determined at one flow predict fish distribution at another flow? If not, then the instream flow incremental methodology (IFIM) will not be useful for evaluating the effect of different flows on fish.

We attempted to validate flow-independent preference by evaluating preferred combinations of depth and velocity (P[*dv*]) in the context of IFIM. In IFIM, P[*d*] and P[*v*] are multiplied together with preference for substrate or cover to determine the value of different microhabitats. We did not evaluate substrate or cover but used P[*dv*] as an indicator of microhabitat quality, as we had done successfully at a flow similar to the preference determination flow (Beecher et al. 1993). We set out to evaluate whether the interaction of habitat preferences and habitat availability would yield a distribution of fish that was consistent with conventional applications of IFIM. If habitat is important to fish and fish select habitat based on its quality, then fish should use higher-quality habitat (higher P[*dv*], equivalent to greater weighted usable area, WUA) more than they use lower-quality habitat if they are not crowded. Behavioral dominance and other intra- and interspecific pressures affect fish distribution within a stream, but we think such confounding effects on preference determination are stronger at high fish densities. The fish in our study were not crowded and left many P[*dv*] cells unoccupied (to which Jager and Pert object). Thus, fish should have occupied high-P[*dv*] cells more frequently than low-P[*dv*] cells, which they did.

Williams proposes that the best test of a change (or lack of change) in depth and velocity preference with a change in flow is to compare the fish distributions, presumably with a goodness-of-fit test. We agree both that this would be a good test of change in preference and that it would require a much larger sample size; at a minimum, the smaller sample should be similar to the larger sample, which was 104 fish for the low-flow determinations. Jager and Pert suggest sampling with replacement and use of different tests to compare preferences at different flows (or sites or seasons). We do not disagree, but although their statistical tests are more powerful than ours, we are not convinced they are suitable for answering the question we asked.

Multiple combinations of depth and velocity can produce the same P[*dv*] value, as noted by Williams, Jager, and Pert. This does affect the distribution of P[*dv*], and it implies an assumption of IFIM that fish respond to a composite of habitat variables rather than to one at a time. We do not see that it affects the logic of our study, however. Our study was prompted by Shirvell's (1990) finding that steelhead parr used different combinations of depth and velocity at different flows. Was the apparent change in velocity use the result of a change in preference or of a change in the combination of depths and velocities that optimized P[*dv*] among available conditions? If the change in depths and velocities occupied resulted from a change in available combinations of depth and velocity alone, then distributions of the fish should be predictable from the original depth and velocity preferences. If the preferences for depth and velocity changed significantly, then we would expect a poor match between fish and their preferred combinations of depth and velocity. For any given value of P[*dv*], once the value of either P[*d*] or P[*v*] is known, the other is known. We found few locations where both P[*d*] and P[*v*] were near 1.00. In many locations P[*d*] was 0.00, resulting in many cells with P[dv] = 0.00. Some of the P[d] and P[v] bands were wider than others, so several individual values of depth and velocity could lead to the same P[dv]. Jager and Pert make a distinction between P[dv] and P[d,v], but we have not seen studies that made a clear biological distinction between them.

We share Williams' concern for the "city-skyline shapes of the preference curves," and we would (and do) smooth these curves for water management use. We have since developed a composite set of depth and velocity preference curves for steelhead parr from the Morse Creek data set, two sets from the Dungeness River, and other sets from other Washington streams (unpublished). The patterns from our Morse Creek curves holds true in the larger data sets (about 1,000 fish observations in each), but transitions between adjacent intervals are smoother. However, for the purpose of testing the preferences for predicting fish distribution, we felt it was more appropriate to use the data as they were rather than to superimpose our own judgments about the nature of the underlying biological response to depth and velocity. Small samples (and 104 fish distributed among 10 depth and 13 velocity intervals constitutes a small sample) are unlikely to represent the population with complete fidelity. In an adjacent stream (Dungeness River; unpublished data), we found differences in the depth and velocity preferences of steelhead parr between two flows, as did Pert and Erman (1994) for rainbow trout *O. mykiss*. Did these reflect true differences in preference or consistent preferences interacting with a different set of available depths and velocities? We cannot rule out the latter, which we believe requires a less complicated behavioral mechanism than preferences that change with flow.

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ASSESSMENT OF CLIMATE CHANGE AND FRESHWATER ECOSYSTEMS OF THE ROCKY MOUNTAINS, USA AND CANADA

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ABSTRACT

The Rocky Mountains in the USA and Canada encompass the interior cordillera of western North America, from the southern Yukon to northern New Mexico. Annual weather patterns are cold in winter and mild in summer. Precipitation has high seasonal and interannual variation and may differ by an order of magnitude between geographically close locales, depending on slope, aspect and local climatic and orographic conditions. The region's hydrology is characterized by the accumulation of winter snow, spring snowmelt and autumnal baseflows. During the 2–3-month 'spring runoff' period, rivers frequently discharge >70% of their annual water budget and have instantaneous discharges 10–100 times mean low flow.

Complex weather patterns characterized by high spatial and temporal variability make predictions of future conditions tenuous. However, general patterns are identifiable; northern and western portions of the region are dominated by maritime weather patterns from the North Pacific, central areas and eastern slopes are dominated by continental air masses and southern portions receive seasonally variable atmospheric circulation from the Pacific and the Gulf of Mexico. Significant interannual variations occur in these general patterns, possibly related to ENSO (El Niño–Southern Oscillation) forcing.

Changes in precipitation and temperature regimes or patterns have significant potential effects on the distribution and abundance of plants and animals. For example, elevation of the timber-line is principally a function of temperature. Palaeolimnological investigations have shown significant shifts in phyto- and zoo-plankton populations as alpine lakes shift between being above or below the timber-line. Likewise, streamside vegetation has a significant effect on stream ecosystem structure and function. Changes in stream temperature regimes result in significant changes in community composition as a consequence of bioenergetic factors. Stenothermic species could be extirpated as appropriate thermal criteria disappear. Warming temperatures may geographically isolate cole water stream fishes in increasingly confined headwaters. The heat budgets of large lakes may be affected resulting in a change of state between dimictic and warm monomictic character. Uncertainties associated with prediction are increased by the planting of fish in historically fishless, high mountain lakes and the introduction of non-native species of fishes and invertebrates into often previously simple food-webs of large valley bottom lakes and streams. Many of the streams and rivers suffer from the anthropogenic effects of abstraction and regulation. Likewise, many of the large lakes receive nutrient loads from a growing human population.

We concluded that: (1) regional climate models are required to resolve adequately the complexities of the high gradient landscapes; (2) extensive wilderness preserves and national park lands, so prevalent in the Rocky Mountain Region, provide sensitive areas for differentiation of anthropogenic effects from climate effects; and (3) future research should encompass both short-term intensive studies and long-term monitoring studies developed within comprehensive experimental arrays of streams and lakes specifically designed to address the issue of anthropogenic versus climatic effects. © 1997 by John Wiley & Sons, Ltd.

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INTRODUCTION

The purpose of this paper is to address the potential effect of climate change on freshwater ecosystems of the Rocky Mountain Region. We examine current climatic conditions and past climate change and hypothesize on future change, within the context of the spatial and temporal variation of this broad geographical region. We consider responses of individual aquatic ecosystems, examine limitations to evaluating climatic change in light of various anthropogenic factors (e.g. river and lake regulation, water abstraction), make recommendations regarding future research and monitoring needs and evaluate the region's suitability as a global indicator of climate change.

The Rocky Mountains encompass the interior cordillera of western North America from the southern Yukon Territory, Canada (63°N) to northern New Mexico, USA (35°N). Many of North American's great rivers (e.g. Athabasca, Colorado, Columbia, Mackenzie, Missouri, Platte, Rio Grande, Saskatchewan, Yukon) have their headwaters in the Rockies. Multiple mountain ranges generally orientate in a north–north-west to south–south-east direction and are characterized by extreme geological and environmental gradients, often in close geographical proximity. Individual ranges frequently contain peak to valley floor elevation differentials greater than 1500 m and exhibit high variance in climate and vegetation. The landscapes reflect both the dynamic geological processes that formed the region, as well as hydrological and glacial processes. The bedrock of sedimentary and igneous origin provides markedly different source material to weathering processes, development of soil and macro- and micro-nutrients contributed to ground and surface waters.

Climatic patterns vary across a variety of spatial and temporal scales within the Rockies. The southern mountains of New Mexico and Colorado have a continental climate, but exhibit high seasonal and interannual variation in the type, frequency and duration of precipitation events (Dahm and Molles, 1992). The northern ranges are dominated by maritime air masses. Weather throughout the Rocky Mountains is modified by local thermodynamic processes that produce distinctive, local microclimates on different slopes and aspects that affect both water and energy fluxes (Barry, 1992).

The Rocky Mountains contain a diversity of freshwater ecosystems. Headwater streams are generally high gradient environments whose channels are controlled by bedrock. Larger streams and rivers, located in the montane valleys, often contain serial sequences of confined and unconfined reaches (Stanford and Ward, 1993). The most prevalent wetlands are associated with seepage slopes, river floodplains or surficial depressions, or the landforms associated with glacial retreat. Tens of thousands of alpine and subalpine lakes reflect a broad array of climatic and geological conditions and biotic histories. Large lakes (e.g. Flathead, Pend Oreille, Kootenay, McDonald) occupy glaciated valleys and are often >100 m deep.

Most aquatic ecosystems of the Rocky Mountains are strongly influenced by highly variable hydrographical regimes. The region is dominated by the annual accumulation of winter precipitation as snow and elevated stream flows in the late spring and early summer (Poff and Ward, 1989). During the 2–3-month 'spring runoff' period, rivers frequently discharge $>70\%$ of their annual water budget and have instantaneous discharges 10–100 times mean low flow (Stanford and Hauer, 1992). Changes in the fundamental climatic variables of temperature and precipitation may affect all aspects of the hydrological regime, including water temperature, discharge, nutrient flux, groundwater and lake levels, sediment transport, ice and snow cover, biological production, food-web dynamics and biogeography (Firth and Fisher, 1992).

REGIONAL CLIMATE

Current climate

Large-scale circulation patterns and their interactions with the Rocky Mountains are well studied. In the northern ranges, weather patterns throughout the year are primarily Pacific maritime, west of the continental divide. Precipitation is closely correlated with cold fronts moving east from the North Pacific and Gulf of

Alaska. Along the east front ranges of western Montana and Alberta continental air masses predominate, particularly during winter, as Arctic fronts with high barometric pressure and cold temperatures move from northern Canada to the Great Plains. Midwinter temperature differentials between maritime and Arctic air masses are often $>40°C$. Thus, during winter, locations are alternatively dominated by different atmospheric sources, and temperature can vary greatly over short time periods. Winter precipitation throughout the Rocky Mountains occurs primarily as snow. Winter snowpacks occur at high elevations that vary with latitude (e.g. *ca.* 2200 m in Colorado, *ca.* 1400 m in Montana). Spring snowmelt increases soil moisture recharge, runoff, groundwater recharge and stream flow. Analysis of spring runoff patterns, precipitation and temperature in western Montana shows that the greatest floods (1911–1990) have occurred in late May or early June following a cool, wet spring and were the result of warm, rain-on-snow events at high elevation (Hauer, 1991).

In more southern ranges, such as the Front Range in Colorado, sources of moisture vary from predominantly Pacific origin during the winter, to a southerly and south-easterly source in the summer (Barry, 1973). Spring precipitation maxima are apparent at low elevations, while autumn and winter maxima are observed near the continental divide. Summer precipitation arises from advective cooling and can occur either as rain or snow at the higher elevations. Severe summer thunderstorms can cause floods up to elevations of *ca.* 2300 m in the Colorado Front Range (Jarrett, 1990). Analysis of flow data over a 60- and 68-year period from two New Mexico rivers shows that spring flows during snowmelt were significantly increased during El Niño years (elevated sea surface temperature and reduced barometric pressure in the eastern tropical Pacific) and significantly reduced during La Niña years (reduced temperature and elevated barometric pressure). This pattern suggests a linkage between accumulations of winter snowpack in the southern Rockies with ENSO (El Niño–Southern Oscillation) phenomena (Molles and Dahm, 1990).

Precipitation and temperature patterns throughout the Rockies exhibit a characteristically high spatial diversity. For example, some west-facing slopes in the Flathead Basin, Montana, have average annual precipitation >150 cm. Other areas only a few km distant average <15 cm per year. The Rocky Mountains are also known for high intra-annual variance in precipitation. This is particularly significant when low soil moisture content during midsummer leads to dry forest conditions and wildfire. An important structuring mechanism in Rocky Mountain forest vegetation is susceptibility to wildfire and the resulting mosaic of vegetation types and ages [for reviews see *BioScience*, 1989, **39**(10)].

Past climate change

Evidence of post-glacial climatic change in the Rocky Mountains has been obtained from three sources; palaeoecological analyses of lake sediments, climatic inferences from various palaeochrono sequence data (e.g. tree-rings, moraines, sediment laminae) and direct instrumental observations. These sources differ in the length of record, temporal resolution, interpretability and sensitivity. Climatic reconstructions from lake sediments record long-term climatic trends over broad time-scales (i.e. the Holocene). However, fossil data are difficult to interpret because identification of the climatic drivers is ambiguous. Furthermore, ancient climatic change may have arisen because of different forcing mechanisms from those that occur today. Consequently, high-resolution palaeoecological and tree-ring analyses over intermediate time-scales (*ca.* 100–1500 years) may provide the greatest insights into the effects of climatic change within montane ecosystems. Such meso-scale analyses are often annually resolved and record regional rather than local environmental changes (Leonard, 1986a). In contrast, instrumental data are the most precise and easily interpreted, but reflect relatively high variance as a result of local phenomena (e.g. cloud cover, localized rainfall). Additionally, these data are comparatively short (<100 years).

Much of what is currently known about Holocene environmental change was first identified by palaeoecological studies in the Rocky Mountains (reviewed in Luckman, 1990). Although those investigations are relatively few, they show remarkable consistency in the pattern of post-glacial climatic change. Recent studies have confirmed that glaciers in the main ranges of the central Canadian Rockies quickly receded between 11 500 and 10 000 years before present (BP) (Reasoner and Rutter, 1988; Reasoner and Hickman, 1989; Reasoner *et al.*, 1994). The onset and rate of glacial recession depended on latitude, elevation, aspect and longitudinal position within the mountain ranges (Luckman, 1990; Hickman and Schweger, 1993). In general, early Holocene climates were considered to be significantly warmer (1–1·5°C) than at present and were maintained for a period of between 1000 and 5000 years, depending on the region (Luckman, 1990). This hypsithermal period was followed by climatic cooling over several millennia, reaching near-present conditions by *ca.* 4000 BP. At least three neoglacial periods have been identified over the last 3000 years, with the most pronounced beginning *ca.* 800 BP and reaching its maximum extent in the mid-eighteenth century and mid- to late-nineteenth century (Little Ice Age). Since 1850, temperatures have appeared to increase, although there is considerable variation between sites (Luckman, 1990).

Climatic change at the start of the Holocene may be an excellent analogue for forecasting a response to global warming. In some cases, glacial retreat occurred over a few decades, rather than centuries as previously supposed (Reasoner *et al.*, 1994). The magnitude and speed of inferred change is similar to projected changes arising from elevated CO_2 concentrations. Recent research suggests that glacial retreat may have consisted of at least two phases, separated by a cold period of up to 1000 years. This cold period is well known from Europe (i.e. the Younger Dryas), and other northern Atlantic regions, and has recently been verified in western North America (Reasoner *et al.*, 1994).

Most evidence of early Holocene climatic warming comes from changes in the species composition of plant macro-fossils, pollen and spores. In particular, physical remains from vascular plants (e.g. boles, needles, seeds) have been useful because they are not subject to long-distance transport like pollen, and because they can be used in accelerator mass spectroscopy (AMS) ^{14}C determinations of sediment age. Transitions from herbaceous, tundra-like communities (e.g. *Artemisia*) to forests of *Pinus* and *Abies* (fir) mark the retreat of glaciers and the stabilization of hillslopes as a result of tree colonization. Lake sediments of this era are often very inorganic because of elevated concentrations of glacial silt ('flour') and carbonates (Reasoner and Hickman, 1989; Reasoner *et al.*, 1994). In fact, the inverse relation between sediment organic content and glacier activity has been proposed as a palaeoclimatic marker of glacial activity (Leonard, 1986a, b).

Temperatures may have continued to rise after the initial glacial retreat (*ca.* 10 000 BP) to reach a post-glacial maximum *ca.* 8000 BP. Inferences of warmer temperatures are derived from analyses of fossil pollen and plant macro-fossils, the presence of buried trees in present day alpine meadows and increased organic content of lake sediments. High relative abundance of fossils from presently lower elevation taxa (e.g. *Abies*, *Picea*, *Pinus*) are interpreted as indicating warmer and perhaps drier conditions. When calibrated to current tree-line distribution and composition (Beaudoin, 1987), these pollen ratios can be sensitive indicators of timber-line migration (e.g. Reasoner and Hickman, 1989). In general, tree-line occurs as the 10°C July isotherm in the central Rocky Mountains and migrates approximately 150 vertical metres or 100 latitudinal km for every 1°C change (Luckman, 1990 and references within). However, comparisons of fossil profiles from paired alpine and subalpine lakes suggest that changes in terrestrial vegetation were most dramatic at alpine, rather than subalpine or montane sites (Hickman and Reasoner, 1994).

Climatic cooling in the Rocky Mountain Region after the mid-Holocene temperature maximum was relatively slow in comparison to earlier warming during glacial retreat. Analyses of fossil pollen ratios and macro-fossils suggest declining tree-line elevations (Reasoner and Hickman, 1989). Increased carbonate and mineral contents of lake sediments indicate that the extent of glaciers increased during the same period (Leonard, 1986a, b). The rate and extent of forest change appears to be site specific, depending on the presence of glaciers within the catchment, lake elevation, lake basin aspect and the responsiveness of the vegetation (e.g. herbs vs trees). In general, most reconstructions suggest that the climate cooled, and perhaps became wetter, until *ca.* 4000 BP when an approximately present day climate was established (Luckman, 1990).

Temperatures during the last two or three millennia have probably been colder than at any time since the start of the Holocene. Throughout this period, alpine lakes with glaciers in their catchments are characterized by highly inorganic, carbonate-rich sediments containing few macro-fossils from trees

(Reasoner and Hickman, 1989; Reasoner *et al.*, 1994). Leonard (1986a, b) calibrated annually laminated sediments with glacial meltwater patterns and showed that the deposition of glacial silts was proportional to the extent of glacier cover within the catchment when averaged over a century. Fossil reconstructions suggested that temperature minima were reached during 1200–1300 AD and 1600–1900 AD, and maximum extent of ice occurred during the 'Little Ice Age' in the mid- to late-nineteenth century.

Highly detailed information on climatic change in the last millennium has been gathered from a wide variety of sources. Neoglacial moraines can be aged and provide data of maximum extent of glacial ice within the Holocene. More detailed information can be gained by analyses of annual lake sediment accumulation (see above) or tree growth patterns. Ring width, wood density and isotope content in timber-line trees are all highly correlated to mean summer temperature (Luckman, 1990). Many trees at tree-line can live over 600 years and records can be further extended using downed trees that have been well preserved. In general, analyses from central Rocky Mountains suggest that the climate has been steadily warming since *ca*. 1850 AD, the start of the earliest instrumental records (Luckman, 1990).

Comparison of long-term instrumental data from closely located sites illustrates that, while there are some overall similarities, recent climatic change is dominated by high interannual variability. For example, comparison of mean annual temperatures from five locations in Banff and Jasper National Parks (Alberta, Canada) showed that temperatures were above average during 1920–1945 and through the 1960s and the late 1980s. However, only one site (Banff) showed a statistically significant warming over the last 100 years. It is unclear whether this reflects a stable climate or statistical insensitivity owing to high interannual variation. Interestingly, temperatures at three sites during the late 1980s were near-historical maxima, a pattern also seen immediately to the east in Edmonton, Alberta (Luckman, 1990).

Evaluating future climate change

The preferred method for estimating the effects of climate change on freshwater ecosystems is the use of output from general circulation models (GCMs) to derive input data sets for surface hydrological models (e.g. US EPA, 1989). This approach has been applied in a variety of studies aimed at assessing the sensitivity and response of lakes (e.g. Croley, 1990; McCormick, 1990; Hondzo and Stefan, 1993) or stream flow (Gleick, 1987, 1989; McCabe and Ayers, 1989; Lettenmaier and Gan, 1990) to global warming. GCM output is usually expressed as a climate anomaly, or as a difference between control and hypotheses-oriented simulations (e.g. doubled CO_2) or to observed data (e.g. a 2°C air temperature added to the observed average air temperature values). Modelling studies incorporating GCM output are mainly useful for establishing first-order sensitivities of freshwater ecosystems, rather than as a basis for detailed projections.

A primary limitation to the use of GCMs in evaluating climate change is their coarse spatial resolution. Typically, GCMs differentiate at spatial scales covering several degrees of latitude and longitude. Existing supercomputers are incapable of implementing models at finer resolution for extended climate simulations. Consequently, most GCMs accurately simulate annual and seasonal climate, but are less reliable in simulating regional spatial- and temporal-scale features that are essential for climate change assessment (Mearns *et al.*, 1990; Grotch and MacCracken, 1991; US EPA, 1991; Hostetler, 1994; Bates *et al.*, 1995). This is particularly true for the Rocky Mountains, where the topography is poorly represented and the model output is very different from the true climate of the locale. For example, in one GCM the topography for the western United States is simulated as a gently sloping mountain originating on the Pacific coast and coming to a point over Utah (Giorgi and Mearns, 1991). Furthermore, the output from different GCMs varies significantly (e.g. Grotch and MacCracken, 1991; US EPA, 1991), posing the problem of which GCM to select for ecosystem assessments.

One approach to resolving the scale problems of GCMs has been to nest a higher resolution or regional climate model (RCMs) within a GCM (Dickinson *et al.*, 1989; Giorgi and Bates, 1989; Giorgi *et al.*, 1990, 1993a, b; Bates *et al.*, 1993, 1995). In this configuration, the GCM is run first, and the initial and lateral boundary conditions for the RCM are derived from the output of the GCM. The RCM is then used to provide high resolution simulations of climate over a limited area at horizontal resolutions of tens of kilometres. The use of RCMs appears to hold some promise for attaining simulations of regional climate and surface hydrology that are relevant to the complex topography of the Rocky Mountains (Running and Nemani, 1991; Giorgi *et al.*, 1993a; Hostetler and Giorgi, 1993). However, the quality of a simulation attained from an RCM depends strongly on the ability of the driving GCM to simulate correctly the timing, location and characteristics of synoptic-scale atmospheric features (Hostetler, 1994).

Given the problems inherent in GCMs and nested RCMs, researchers have resorted to alternative approaches to evaluate future climate change. One of the most widely used methods has been to estimate average annual changes in precipitation and temperature using GCMs and then to apply these estimates to adjust historical meteorological time-series data. In the simplest case, the adjustment is made by increasing historical precipitation values by a fixed percentage. Hypothetical scenarios using instrumental estimates of climate change, instead of GCM results, appear to be most promising for the highly variable topographies and microclimates of the Rocky Mountains.

STREAM AND RIVER ECOSYSTEMS

The streams and rivers of the Rocky Mountains are dynamically linked to basin geomorphology, climatic–hydrological regimes and ecological processes and patterns (Hynes, 1975; Minshall, 1988; Reice *et al.*, 1990; Burt, 1992; Stanford and Ward, 1993). Biotic and abiotic stream characteristics change along extreme elevation gradients that are analogous to those seen along latitudinal gradients (see Hauer and Stanford, 1982a; Stanford *et al.*, 1988; Sweeney *et al.*, 1992). Terrestrial ecologists have recognized for over a century the relationship between vegetation composition and elevation within montane regions (Merriam, 1890). Such clinal changes also exist in lotic ecosystems and include changes in thermal regime, bed and channel form, hydrological variability, biogeochemistry and the structure and function of biota along the stream corridor.

Hydrology and temperature regimes

The hydrology of the Rocky Mountain Region is dominated by snow accumulation and melt (Poff and Ward, 1989). Precipitation, in the form of snow, is normally accumulated during winter and released as snowmelt during summer. At mid-continental latitudes, high elevation snowpacks generally begin in mid-autumn and persist until late spring and even into summer (Turk and Spahr, 1989; Baron, 1992). The volume of water stored in snowpack is highly variable but generally increases with increasing elevation. Snowmelt and runoff typically being in March or April, reach a peak in May or June and recede to baseflow conditions in July or August. Convective thunderstorms may produce late spring flooding, particularly when rain on snow conditions occur (Hauer, 1991). During the late summer and autumn, streamflow is predominantly supported by groundwater discharge.

Diurnal variations in stream flow during the snowmelt period are very dynamic (Figure 1). Changes in discharge reflect the variation in meteorological variables that drive the melt process (e.g. solar radiation, air temperature). Daily snowmelt also moves vertically to recharge groundwater, both within and over the unsaturated soil zone. In some areas, the water table reaches the soil surface and groundwater discharge becomes surface runoff (e.g. seepage–slope wetlands and spring brooks) before reaching a stream channel. As stream size and discharge increase, diurnal variation around the mean daily discharge is somewhat reduced.

Mountain streams have several types of flow regimes. For example, snowmelt streams flow throughout the late spring and summer and are supplied by surface snowmelt, groundwater from saturated soils and snowmelt waters moving rapidly through unconsolidated till and talus. Both permanent and ephemeral snowmelt streams are characterized by low concentrations of suspended particulates, dissolved nutrients and dissolved organic compounds (Hauer and Stanford, 1982b). In contrast, glacial outwash streams receive their waters primarily from glacier ablation and have continuous stream flow throughout the summer. Similarly to snowmelt streams, glacial streams also tend to be low in nutrients and dissolved organic

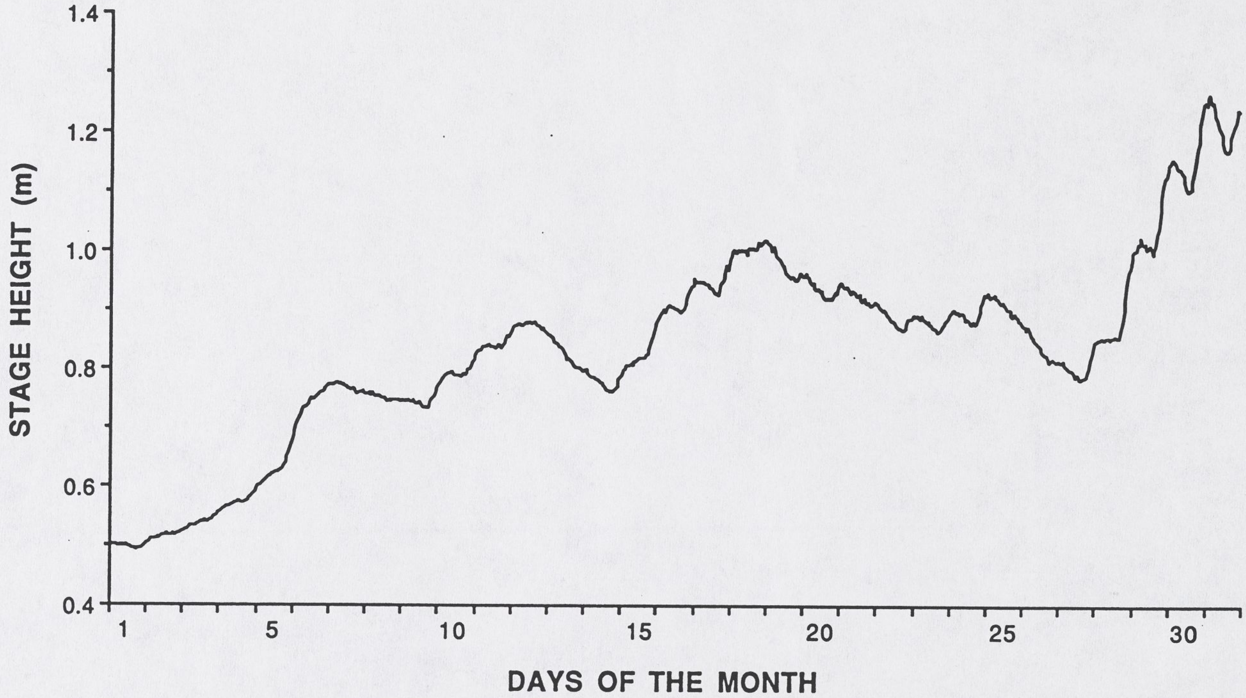

Figure 1. Mean hourly stage height recordings (m) for 1–31 May 1995 in McDonald Creek, Glacier National Park, Montana, USA. Note change in discharge throughout month as well as diel change

compounds, but generally have high concentrations of inorganic particulates (glacial flour). Changes in snow accumulation in winter or changes in the rate of snowmelt in summer would directly affect the hydrological regime of mountain streams, whether they are snowmelt fed (e.g. permanent streams becoming ephemeral with a decrease in snowpack) or glacial fed (e.g. rapid glacier ablation and disappearance).

Changes in temperature are likely to affect montane stream ecosystems through a broad influence upon precipitation state (i.e. snow vs rain), the rate of snowmelt, biogeochemical flux rates and the rate of the metabolic functions of biota. Montane stream temperatures (e.g. annual degree–days, summer mean, summer maximum) are closely correlated with elevation and stream size (e.g. Figure 2), although temperatures may vary significantly between alpine sites. For example, water temperatures may remain near 0°C for north-facing groundwater, surficial snowmelt or glacial sources, whereas temperatures in streams on south-facing slopes may rise as much as 16°C because of direct solar radiation (F. R. Hauer, unpublished data). In contrast, summer temperatures in subalpine streams generally remain <10°C in forested areas, while third- and fourth-order streams generally reach 10–15°C. Large montane valley rivers (fifth to seventh order) experience direct solar radiation and summer maximum temperatures between 18 and 24°C (Hauer and Stanford, 1982b; Stanford *et al.*, 1988).

Climate warming may significantly alter surface and groundwater temperatures. Warmer atmospheric temperatures should particularly affect streams that do not receive direct solar radiation and are more influenced by air temperatures. However, it is unclear whether projected climate change would result in a generalized warming trend throughout the Rocky Mountain Region, or whether change would be strongly regionalized. Furthermore, weather patterns and the influences of storms and cold fronts may have a profound effect on hydrological output (Dahm and Molles, 1992) and thermal regimes, particularly at mid-continental latitudes where maritime influence is most acute.

Fluvial processes, hyporheic habitats and floodplain development

Glaciation has dramatically affected landforms throughout the Rocky Mountain Region (Alt and Hyndman, 1973). Arêtes, glacial cols, cirque headwalls, horns and other erosional landforms of valley

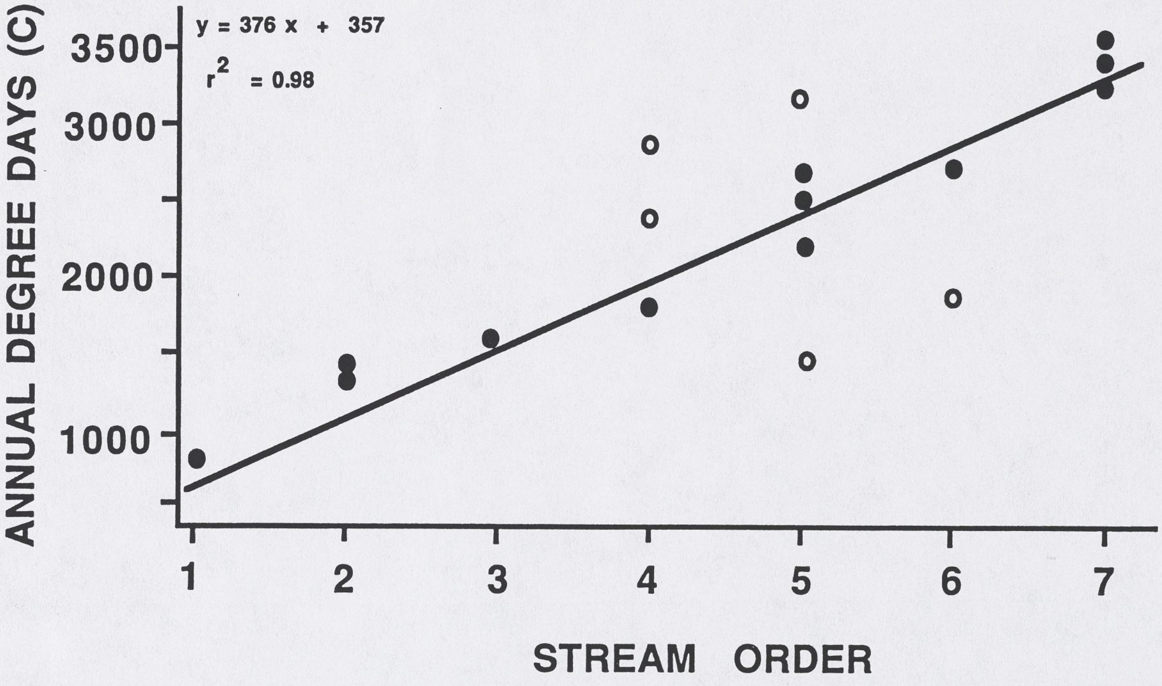

Figure 2. Relationship between temperature [expressed as annual degree days (°C)] and stream order at a series of stream sites in the Flathead Basin, north-western Montana. Solid circles represent sites along the river continuum from high elevation, small streams to low elevation, large rivers. Open circles represent sites below lakes (warmed) or hypolimnion release hydropower dams (cooled). Linear regression is taken only from solid data points. (Modified from Stanford *et al.*, 1988)

glaciers characterize much of the region. Small, high elevation streams generally possess turbulent flow along steep gradients under bedrock control of bed and channel form. Upon reaching the valley floor of the glacial trough, streams frequently descend a series of steps (i.e. glacial stairway) forming confined and unconfined reaches. Low gradient, unconfined reaches are often filled with alluvium. These river segments are characterized by extremely porous substrata saturated by river water that flows interstitially through a network of palaeochannels distributed across the floodplain, creating extensive hyporheic habitats (Stanford and Ward, 1988). Palaeochannels form a vertical lattice of substrata created by the chrono-sequence of laterally abandoned main channels that have become buried by fine sediments deposited by surficial flooding (Stanford and Ward, 1993). Palaeochannels act as conduits of interstitial water as a function of the vertical hydraulic gradient of the flood plain and are often an integral part of the hydrogeomorphology of riparian wetlands. Phreatic (deep) groundwaters may enter the floodplain from unconsolidated glacial till and colluvium along the valley wall and mix into floodplain aquifers. Interstitial flow of water from the main channel, or from tributaries, delimit the hyporheic zone (Stanford and Ward, 1993). Likewise, regular flooding of the river floodplain maintains surface and subsurface connectivity between the main channel, hyporheic habitats and riparian wetlands of the gravel-bed river systems.

Climate change affecting the magnitude and frequency of flooding will directly and indirectly affect these river flood plains. Climatic warming, leading to reduced winter snowpack, would result in a lower total discharge and, generally, a lower peak in spring runoff. Since the annual spring flood is primarily responsible for the redistribution of alluvium as well as stream channel development (i.e. creating new channels and abandoning old channels), reduction in the frequency or intensity of flooding would reduce the long-term complexity of the floodplain. Changes in the timing and magnitude of flooding will directly affect the flux of water, materials (e.g. nutrients, sediment, organic carbon) and biota between the main channel, hyporheic habitats and riparian wetlands. The complexity of these structures and the degree of their interactions directly affect stream corridor biodiversity and ecosystem integrity (*sensu* Angermeier and Karr, 1994).

Biogeochemical flux and cycles

Alpine and subalpine biogeochemical fluxes are strongly controlled by snowmelt. Mass flux through alpine watersheds is dominated by snowmelt runoff, which typically results in $\geqslant 70\%$ of the flux of water the solutes during May–July. Solutes in surface waters are dependent on atmospheric inputs, hydrological flow paths, mineral weathering products, soil chemistry and hydrological temporal dynamics (Campbell *et al.*, 1995). Processes in the terrestrial ecosystem strongly influence inputs to the aquatic ecosystem. Solutes stored in snow from the previous winter are transported over snow and ice, into and through soils and enter surface and ground waters. Vegetation frequently has an important influence on the biogeochemical cycling of carbon, nitrogen and many other nutrients (e.g. Mast and Baron, 1990; Running and Nemani, 1991; Baron, 1992; Arthur and Frahey, 1993).

The potential effects of climate change on biogeochemical fluxes in alpine and subalpine aquatic ecosystems would most likely be caused by shifts in the magnitude and timing of snow accumulation, snowmelt runoff and in the proportion of snow or rain. Biogeochemical reactions in the soil and groundwater have substantial effects on water chemistry only after snowmelt is mostly complete (*ca.* July–August). Yet, by late August, night temperatures frequently fall below freezing, and terrestrial biological activity beings to slow. This makes alpine watersheds sensitive indicators of climate change, because even small changes in temperature or precipitation could cause substantial changes in the duration of the late summer period when conditions are favourable for biogeochemical cycling.

The precise response of biogeochemical processes in lotic systems to climate change will be difficult to predict. For example, the source of stream water during snowmelt includes both direct snowmelt and displacement of 'old' subsurface water. Preferential elution causes early snowmelt water to be acidic and rich in solutes such as nitrate and sulfate that are found in atmospheric deposition. In contrast, the displaced subsurface water is often well buffered and rich in weathering products. An increase in direct snowmelt may favour the acidic components, thus increasing the risk of episodic stream acidification. Alternatively, high elevation systems may become more productive owing to increased maximum summer temperatures, longer growing season, longer water retention times and increased atmospheric loading of essential nutrients.

Lotic biota

A fundamental feature differentiating alpine from lower elevation streams is the character of the stream-side vegetation. Alpine streams, being above the timberline, receive direct solar radiation and have few allochthonous inputs from riparian vegetation. Lower elevation streams have woody streamside vegetation that shades the stream, although sources of allochthonous material may be small and highly refractory (Triska and Sedell, 1976). Montane valley streams also contain large woody debris that influence transport and retention of organic matter and the trophic relations of benthic invertebrates (Bilby, 1981; Anderson *et al.*, 1984; Malanson and Butler, 1990; Ralph *et al.*, 1993). Climatic change leading to elevation change in the timberline would have a profound effect on the structure and function of alpine stream systems. For example, energy budgets of high elevation, open canopy streams tend to be primarily autochthonously based. The trophic relationships between the benthic fauna of these streams are dominated by grazers andcollector-gatherers (*sensu* Merritt and Cummins, 1996). Small streams below the timber-line (i.e. closed canopy) are allochthonously based, with benthic fauna dominated by collectors (e.g. net-spinning caddis-flies), collector-gatherers (e.g. ephermerellid mayflies) and predators (e.g. perlid stone-flies).

Many factors influence the distribution and abundance of stream invertebrates along elevational gradients (Hauer and Stanford, 1982a, 1991; Hawkins, 1984; Stanford *et al.*, 1988), especially temperature (Ward and Stanford, 1982). Most lotic invertebrates have well-defined distributions that reflect the close linkage to temperature (Sweeney, 1984). For example, many species of the caddis-fly family, Hydropsychidae, undergo serial replacements along elevation gradients (Figure 3), even though each species performs the same ecological function (filtering seston using a silk net). Thus, changes in stream temperatures are expected to affect species-specific distributions. In high alpine environs, cold stenothermic species may be extirpated if

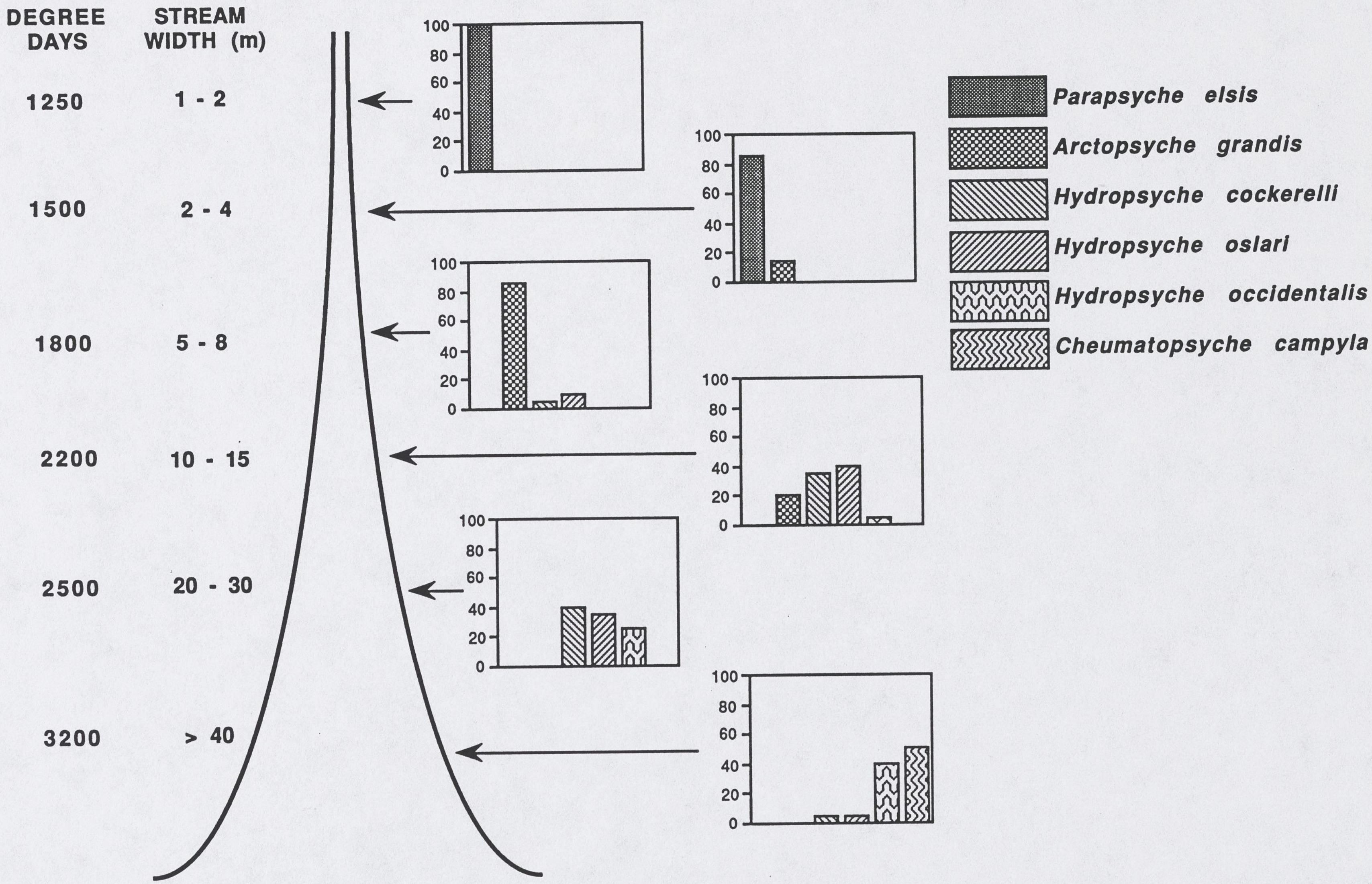

Figure 3. The distribution and relative abundance (percentage of total composition) of the six commonly occurring net-spinning caddis-flies (Trichoptera: Hydropsychidae) as they occur along the river continuum and elevation and temperature gradient in Rocky Mountain streams of southern British Columbia and Alberta, and western Montana. Note the species replacement from *Parapsyche elsis* in the small, cold streams to *Cheumatopsyche campyla* in the large, warmer rivers

temperatures rise beyond tolerable limits or if precipitation changes result in a stream becoming intermittent. Thus, changes in organic matter sources, temperature or hydrological flows and regime would have a profound effect on zoobenthic biodiversity and system integrity.

Native fish populations in cold streams of the Rocky Mountains are, generally, numerically dominated by salmonids. Native salmonids originally consisted of subspecies of cutthroat trout (*Oncorhynchus clarki*; see Behnke, 1992), along with combinations of bull char (*Salvelinus confluentus*), mountain whitefish (*Prosopium williamsoni*) and Arctic grayling (*Thymallus arcticus*) in the northern ranges. In the southern Rocky Mountains of Arizona and New Mexico, Gila trout (*O. gilae gilae*) and Apache trout (*O. g. apache*) are the native salmonids. However, non-native brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*) and rainbow trout (*O. mykiss*) have been introduced throughout the region (e.g. Fausch, 1988, 1989).

Temperature is also an important environmental factor structuring salmonid guilds along altitudinal gradients (Fausch *et al.*, 1994). Modified thermal and hydrological regimes resulting from climatic changes should have both direct and indirect effects on stream salmonds. For example, Keleher and Rahel (1996) estimated that 62% of the geographical area suitable for salmonids in the Rocky Mountain Region would become too warm, and 31% of stream length suitable for salmonids in Wyoming would become unsuitable, with a 4°C warming in air temperature. This is consistent with the results of Meisner (1990, 1993) and Flebbe (1993) regarding the effect of groundwater warming on salmonid distributions in the southern Appalachian Mountains.

Changes in the stream discharge regime may have marked direct effects on salmonid reproduction. Native salmonids are either early summer spawners, adapted to lay eggs and complete juvenile emergence on the descending limb of the snowmelt hydrograph (e.g. cutthroat trout), or autumn spawners that incubate eggs during winter and emerge the following spring before runoff (e.g. bull char). An increase in rain on snow events owing to winter warming would affect incubating eggs of autumn-spawning salmonids (e.g. Seegrist and Gard, 1972; Erman *et al.*, 1989), whereas reduced summer flows would alter recruitment of all species (Northcote, 1992). Similarly, high snowmelt runoff may depress recruitment of recently emerged juveniles (Nehring and Anderson, 1993).

Climate warming may have a number of subtle, indirect effects on stream salmonids. Highly plastic life histories have permitted salmonids to adapt to diverse habitats. For example, fluvial cutthroat trout and bull char spawn and rear in small streams, but move downstream to grow and mature in larger rivers. Adfluvial forms also spawn and rear in small streams, but grow and mature in large lakes (Varley and Gresswell, 1988; Fraley and Shepard, 1989; Rieman and McIntyre, 1993). Both fluvial and adfluvial forms are known to move relatively long distances to complete their life history (Gowan *et al.*, 1994; Young, 1994; Riley and Fausch, 1995; Schlosser and Angermeier, 1995), and are likely to be linked as metapopulations by dispersal (Fausch and Young, 1995). Fish populations in headwater habitats may often be extirpated by stochastic perturbations [e.g. fire, floods (Propst *et al.*, 1992)], but were probably recolonized from downstream populations (Harrison, 1991). However, if climate warming eliminates downstream source populations, headwater subpopulations will most likely collapse (Flebbe, 1993).

Climate warming may also affect stream salmonids by exacerbating biotic interactions with non-native species. In many locales, native cutthroat trout have been excluded from their natural stream habitat by introduced brook trout and brown trout (Griffith, 1988; Fausch, 1989). Recent laboratory experiments showed that brook trout behaviourally dominated cutthroat trout and garnered more food at 20°C, whereas competitive abilities were similar at 10°C (DeStaso and Rahel, 1994). Thus, warming of otherwise appropriate stream habitat could provide non-native trout with a competitive advantage.

LAKE ECOSYSTEMS

Montane lakes may be subject to many of the effects of climate change identified elsewhere in this volume. Possible changes in the physical characteristics of lakes include: temperature structure and mixed layer depth, summer and winter heat budgets, timing of the onset and breakdown of both summer and winter stratification, timing of the onset and break-up of ice cover, river through-flow pattern and drainage basin storage and flushing and ventilation rates. In addition, mountain lakes may have a number of unique responses to warming, which vary both with lake size and elevation.

High elevation lakes are usually small, ultraoligotrophic, poorly stratified and poorly buffered systems that lack natural populations of fish, macrophytes or insect predators (Anderson, 1974a). Waters have low concentrations of dissolved organic compounds (Baron *et al.*, 1991), are transparent to UV radiation and may be either clear, or turbid, depending on the local importance of glaciers. Their planktonic food-webs are dominated by low densities of large (>3 mm) brightly coloured predacious copepods (*Diaptomus*, *Hesperodiaptomus*), large herbivores (*Daphnia pulex*, *D. middendorfianna*) and several species of rotifers, flagellates, diatoms and cyanobacteria (McKnight *et al.*, 1991; Stockner, 1991; Thomas *et al.*, 1991). Low maximum summer temperatures (e.g. <12°C) may restrict successful colonization by many temperate species (e.g. Lamontange and Schindler, 1994). Benthic communities frequently support high densities of *Gammarus* (Leavitt *et al.*, 1994) and benthic cyanobacteria, *Chara*, or *Cladophora* (Stanford and Prescott, 1988), but have relatively depauperate chironomid communities (Walker and Mathewes, 1989).

Finger lakes (e.g. McDonald, Waterton) and graben lakes (e.g. Pend Oreille, Flathead) are common among the intermontane valleys of the Rocky Mountain Region. These large lakes are generally oligotrophic with low concentration of nutrients (< 1μg/l soluble reactive P) and primary production (10–20 mg/m^2/yr, <1 mg/l Chl *a* standing crop). Phytoplankton populations are generally dominated by diatoms in spring and green algae in summer. Historically, planktonic food-webs have been dominated by large cladocerans and pelagic fishes; however, introductions of non-native invertebrates and fish have significantly affected native populations and food-web structure (Spencer *et al.*, 1991).

Lake hydrology

Most alpine lakes are small and have highly variable hydrology. Lake flushing rates can exceed 0·71 per day in spring (Baron, 1992), but are generally negligible in winter and intermediate in summer. In many montane watersheds, water retention during spring runoff may be very short and lakes are particularly sensitive to change in water budget or change in biogeochemical processes occurring during snowmelt. Changes in the magnitude or duration of snowmelt from climate change would most likely cause a shift in the relative importance of the in-lake biogeochemical processes. Furthermore, high flushing rates select for phytoplankton species with rapid growth rates (e.g. diatoms), whereas cyanobacteria and flagellates often dominate during relatively quiescent late-summer periods (McKnight *et al.*, 1991). Thus, changes in precipitation patterns may dramatically affect hydrology and hence plankton community structure (Thomas *et al.*, 1991).

The long-term hydrological response of lakes with glaciers may be easier to predict. Over a time-scale of 100 years, the input of suspended inorganic matter to alpine lakes is strongly correlated with glacier size and summer temperature (Leonard, 1986a, b). Long-term fossil analyses show that silt input is greatest during paraglacial periods, when glaciers are extensive, but retreating (e.g. Hickman and Reasoner, 1994). Under these circumstances there is a sufficient volume of water for transport of sediments, and recently exposed substrates are unstable because of sparse vegetation cover. Because the recent 'Little Ice Age' included the coldest period since the start of the Holocene, current climatic warming is occurring during such a paraglacial era and water flow and silt loads may be exceptionally high. For example, estimates from the Premier Range in British Columbia suggest that 23% of glacier cover was lost between *ca.* 1850 and 1970, especially from small glaciers. Rates of recession can exceed 50 m/yr (Leonard, 1986b).

The importance of glaciers in hydrological processes should vary across elevational and latitudinal gradients. There are few glaciers and ice fields among the southern Rocky Mountains. However, glaciers may cover over 15% of mountainous regions in the Canadian Rockies (Luckman, 1990). Similarly, glaciers are less common in rain shadow regions or on south-facing slopes than at other sites. For example, Hickman and Schweger (1993) showed that lakes in the eastern Rocky Mountain foothills and plains were initially saline in the early Holocene because glaciers blocked the flow of moist Pacific air. However, as glaciers melted, present day circulation was established, and lakes freshened. In contrast, mountain and intermontane lakes of the

Rockies were fresh throughout the Holocene. Such variability suggests that there are multiple responses of alpine hydrology to climatic warming.

The water budgets of the large lakes in the mountain and piedmont valleys of the Rocky Mountains are controlled by the large snowmelt rivers that flow into them. Most of these lake basins occupy $<5\%$ of their catchments and the calculated retention times are often less than 3–5 years, even though lake depths are often >100 m. Water flux and associated limnological responses have not been well documented over all large lakes. However, in Flathead Lake, Montane, $>60\%$ of the annual inflow generally occurs during the 4–8 weeks of the spring runoff (J. Stanford, unpublished data). Generally, river water during this time is 2–5°C warmer and considerably less dense than lake water, thus spring floodwater may not reside in the lake more than a few days as rivers may exhibit overflow with little mixing of the two water masses. Montane lakes usually exhibit dimictic thermal stratification. However, the very largest lakes (e.g. Flathead, Kootenay, Pend Orielle) do not freeze over unless becalmed for several days during exceptionally cold years. Wind-driven mixing usually keeps the pelagic area ice free, but the entire water column may cool to 1–2°C.

Catchment temperature and precipitation patterns are the principal meteorological factors affecting the limnology of large valley-bottom lakes in the Rocky Mountains. Mixing of water and retention of nutrients are determined in large part by temperature differentials of the incoming river water and in-lake water, as well as interactions with wind energy. Climate change resulting in warmer temperatures and a changed hydrological regime would alter the flux of water, heat and nutrients and thereby influence the seasonal dynamics of phytoplankton composition, responses of zooplankton, fish reproduction and overall bio-production.

Biogeochemical flux and cycling

Primary production in Rocky Mountain alpine lakes is usually limited by a combination of low temperatures, rapid flushing and extremely low phosphorus (P) supply. Concentrations of total P (TP) and chlorophyll (Chl) are often less than 2–5 μg/l in alpine lakes, and are usually less than subalpine sites within the same drainage (but see McKnight *et al.*, 1991). Increased temperatures may lead to increased nutrient loading. Longer ice-free seasons and higher temperatures would immediately increase the rates of mineralization, although this relation may be complicated by changes in precipitation patterns and hydrology (see above). Over longer time scales, the introduction of forest vegetation would improve biotic cycling of nutrients within soils and increase nutrient supply to aquatic systems.

Development of forests at alpine sites should increase the concentrations of dissolved organic matter (DOM) and reduce lake transparency to ultraviolet radiation. UV intensities rise by *ca.* 15% for every 1000 m elevation and thus are high in alpine lakes. However, unlike subalpine sites, alpine lakes have low levels (<2 mg/l) of both autochthonous and allochthonous dissolved organic carbon (DOC) (Baron *et al.*, 1991). Because terrestrially derived DOC from wetlands and soils are the main agents attenuating UV radiation (Schindler *et al.*, 1992), UV-A (320–400 nm) radiation may penetrate to >8 m depth in alpine sites (D. Lean, National Water Research Institute, Burlington, Ontario, personal communication). In addition, the products of UV photochemical reactions (radicals, peroxides) can circulate throughout the water column of unstratified alpine lakes. Consequently, the biota of alpine lakes may exhibit high levels of UV-related stress (e.g. Vincent and Roy, 1993; Williamson *et al.*, 1994). Prolonged climatic warming would allow the development of terrestrial vegetation and soils, increase inputs of DOC and reduce UV penetration.

Production in most large, valley bottom lakes appears to be controlled by the availability of labile forms of phosphorus and nitrogen (Dodds *et al.*, 1989; Dodds and Priscu, 1990; Spencer and Ellis, 1990). Since most large Rocky Mountain lakes have experienced significant change in land use within their drainages during the past 4–5 decades (e.g. increased population, timber harvest), trophic dynamics in these lakes reflect a multitude of environmental changes (e.g. sedimentation rates, nutrient flux, primary production, food-web composition) (Stanford and Ward, 1992).

Warming of mountain climes will most likely change the water, heat, nutrient (C, N, P) and sediment flux in large valley bottom lakes, and the influences of these factors will be interactive with increasing human activities occurring in the catchment basins. For example, extremely diverse communities of crysophytes (diatoms) and chlorophytes (green algae) currently dominate the phytoplankton communities. Human-mediated nutrient loads of C, N and P increase microbial production and result in the eventual predominance of nitrogen-fixing cyanophytes. Oxygen depletions in the deep waters associated with increased C, N and P loading may result, and can affect the redox conditions on the lake bottom, dramatically enhancing internal nutrient loading (Wetzel, 1983). Indications of eutrophication, such as oxygen depletion, have already been observed in Flathead and other lakes (J. Stanford, unpublished data).

Lake biota

The food-webs of alpine lakes are often simple both in terms of the number of trophic levels and the degree of functional redundancy (species per trophic level). Over 95% of all alpine lakes in western North America are naturally fishless (Bahls, 1992). In addition, larger alpine lakes are usually too cold to support predacious insects as *Chaoborus* (Lamontange *et al.*, 1994) or Cladocera such as *Leptodora* (Anderson, 1974a). Instead, fishless lakes are dominated by predacious copepods of the subgenus *Hesperodiaptomus* (Anderson, 1974a), large red copepods that greatly reduce the abundance of rotifers and other small zooplankton (Anderson, 1970; Paul and Schindler, 1994). Herbivore communities are also simple and dominated by large-bodied *Daphnia*, rather than small cladocerans (Anderson, 1974a). Perhaps because of their simple nature, alpine food-webs may be especially sensitive to projected environmental changes.

Climatic change may have its greatest impact on primary production in alpine lakes. Analyses of fossil diatoms (Hickman and Reasoner, 1994) and pigments (P. R. Leavitt, M. A. Reasoner and M. Hickman, unpublished data) suggest that both species abundance and diversity increase as forests develop in alpine watersheds, possibly because of increased ice-free seasons. Analyses suggest that planktonic species may benefit particularly from climatic warming (Hickman and Reasoner, 1994). In addition, rooted macrophytes are rare in alpine lakes, but are present in subalpine and low elevation systems and may benefit from increased water temperatures or growing seasons.

Elevated nutrient inputs from developing terrestrial soils would be expected to boost algal biomass in phosphorus-limited alpine lakes. However, minor changes in nutrient loading may also have unexpectedly large effects on algal species composition and vertical distribution. For example, the phytoplankton of many alpine lakes show significant adaptations to high light intensities. Flagellates and picoplankton often avoid inhibiting irradiance by forming deep water populations, even in deep unstratified lakes (Anderson, 1974b; Stockner, 1991; Thomas *et al.*, 1991). These deep populations are highly sensitive to changes in water chemistry and are rapidly lost upon minor lake fertilization (Stockner and Shortreed, 1991).

Recent experiments have demonstrated that natural levels of UV radiation (300–400 nm) at alpine elevations can suppress growth of attached periphyton $>50\%$ (R. D. Vinebrooke and P. R. Leavitt, unpublished data). However, natural periphyton communities are often dominated by filamentous cyanobacteria in alpine lakes. These taxa can produce unique pigments that allow them to withstand high UV flux (Garcia-Pichel and Castenholz, 1991; Vincent *et al.*, 1993).

Not all phytoplankton will increase under a scenario of climatic warming. Phytoplankton in shallow, rapidly flushed alpine lakes appear to be controlled by hydrological regimes, rather than by changes in invertebrate community structure, nutrient flux or UV exposure (McKnight *et al.*, 1991; Spaulding *et al.*, 1993). Similarly, production may decline in glacier-fed lakes, as increased silt input favours thinly silicified diatoms or small picoplankton over thick benthic mats of *Chara*, *Cladophora* or cyanobacteria. These mats seem to dominate primary production in the most extreme alpine sites (Stanford and Prescott, 1988). Finally, changes in snowpack distribution may lead to unpredictable changes in primary production. Under-ice algal production can be significant through much of the winter if high winds remove most of the snow cover (Pennak, 1968; Spaulding *et al.*, 1993). Altered precipitation or circulation patterns may lead to an increased depth of snow and reduced light penetration in winter.

It is unclear if projected climatic warning would lead to colonization of alpine lakes by species of temporate fish. Most of the 1464 lakes of the Canadian Rocky Mountain National Parks were fishless prior to the twentieth century, or were inhabited by either mountain whitefish (*Prosopium williamsoni*) or longnose suckers (*Catostomus catostomus*). However, 305 lakes were stocked with non-native trout during this century (Donald, 1987). The persistence and abundance of introduced stocks were directly proportional to either the size of the lake outlet or lake depth, depending on the species introduced. In addition, the presence of mountain whitefish, longnose suckers or lake trout (*Salvelinus namaycush*) reduced the probability of colonization. Consequently, there is no simple prediction regarding the likelihood of successful colonization of alpine lakes by fishes resulting from projected climatic change.

Colonization of alpine lakes by fishes as a result of climatic warming would significantly reconfigure alpine food-webs and alter biogeochemical cycles (Leavitt *et al.*, 1994). Size-selective predation by introduced fish was associated with the elimination of large-bodied invertebrate predators (*Hesperodiaptomus*), herbivores (*Daphnia*) and zoobenthos (*Gammarus*) in many alpine lakes in the northern Rocky Mountains (Anderson, 1972, 1974a, 1980). Loss of the top invertebrates predator almost certainly allowed small herbivorous copepods, rotifers and predacious cyclopoid copepods to increase (Anderson, 1972). In small lakes, fish may switch to less preferred prey (terrestrial insects) after extirpation of large aquatic invertebrates, thereby increasing nutrient recycling between the littoral zone and pelagic waters (Leavitt *et al.*, 1994).

Some invertebrates may colonize alpine lakes in response to increased lake water temperature. Palaeolimnological study of invertebrate communities shows that alpine lakes are often inhabited by cold stenotherms with slow growth rates and poor competitive abilities (Walker and Mathewes, 1989). Many invertebrates, important in structuring the pelagic community, are excluded from alpine lakes because of insufficient degree–days to complete life cycles, poor resource bases or inadequate terrestrial (for adults) or aquatic (immatures, larvae) habitats. For example, *Chaoborus* are important invertebrates predators in many lakes (Lamontagne *et al.*, 1994). Small species (*C. punctipennis*) did not occur in lakes where temperatures were $<20°C$ and large species (*C. americanus*) did not occur in lakes where temperatures were $<15°C$. Interestingly, *Chaoborus* were present in shallow, warm alpine ponds, and were rare in cold, low elevation lakes, suggesting that the terrestrial environment was less important than water temperature in controlling species presence (Lamontange *et al.*, 1994). Colonization of *Chaoborus* in lakes at tree-line might lead to significant changes in the invertebrates predation regime and zooplankton community structure.

Benthic invertebrate communities will also be influenced by climatic warming. Walker and Mathewes (1989) showed that the chironomid communities of alpine lakes are depauperate relative to similar subalpine sites. Taxa characteristic of high elevations (*Heterotrissocladius*, *Parakiefferiella*, *Paraclaudius*) were also common in high Arctic sites, deep cold lakes and early Holocene fossil assemblages, again suggesting that water temperature was the dominant control of community composition. Similarly, Donald and Anderson (1980) found that lentic stone-flies were restricted to alpine sites or large, cold subalpine lakes. Such distinct alpine communities probably result from direct temperature limitation of more temperate species, rather than a preference of alpine taxa for cold waters (Walker and Mathewes, 1989). Consequently, lake water warming and species introduction could lead to loss of alpine fauna via competition or predation.

Invertebrate food-webs may be altered as a result of the indirect effects of climatic warming. In cases where invertebrate predators are resource limited, increased production allows the establishment of additional trophic levels (Neill and Peacock, 1980; Neill, 1988) or alternative invertebrate predators. Similarly, increased water temperatures may allow the development of littoral macrophyte beds that are normally absent from alpine lakes.

The biota of the large, valley bottom lakes will be affected by changes in material flux from their upper watersheds. For example, sediment and nutrients entering Flathead Lake in the spring have a significant effect on summer primary productivity; a low peak in spring runoff delivers less C, N and P from the upper basin than do high runoff years, directly affecting both auto- and heterotrophic production (Ellis and Stanford, 1982, 1988). Microbial production is also closely related to light penetration and the depth of summer mixing in large, oligotrophic lakes (Jassby *et al.*, 1992). Consequently, the effects of changing light conditions (e.g. higher UV-B) on photosynthetic efficiency and species composition may be a factor in these large, low-elevation lakes, as well as in the small, alpine lakes.

In general, the large lakes of the region have a long history of food-web changes mediated by the introduction of non-native species. Non-native species have produced both top-down and bottom-up cascading effects on lake trophic dynamics (e.g. Spencer *et al.*, 1991). Many native species, particularly fishes and amphibians, are currently in rapid decline throughout the Rocky Mountain Region (Gresswell *et al.*, 1995; Nehlsen *et al.*, 1991) as a consequence of habitat degradation and food-web change. Climate warming or eutrophication of the valley bottom lakes will exacerbate problems of biodiversity and ecosystem integrity already associated with destabilized food-web structure and enhancement of non-native species populations. Native species that have evolved complex life histories in the cold oligotrophic environs of the large lakes (e.g. bull trout, Fraley and Shepard, 1989; Yellowstone cutthroat trout, Gresswell *et al.*, 1995) are especially vulnerable.

CONFOUNDING FACTORS

The effects of resource management are felt throughout the Rocky Mountain Region. In many locations these disturbances may obscure or entirely mask the effects of climate change. Deforestation and mining have produced acute, localized perturbations with deleterious effects on downstream freshwater ecosystems. Air pollutants are more diversified, but result in chronic and episodic effects to both terrestrial and aquatic systems, especially in poorly buffered, high elevation habitats (Turk and Spahr, 1991; Baron, 1992; Baron and Denning, 1993). To date, the most pervasive anthropogenic factors affecting freshwater ecosystems within the Rocky Mountain Region are: (1) alterations of land use that increase erosion and nutrient mobilization; (2) construction of dams and diversions that alter hydrological and thermal regimes and interfere with the movement of materials and biota; (3) introduction of non-native species that reconfigure food-webs; and (4) urbanization and the associated nutrient enrichment.

Runoff of sediment and nutrients from agricultural lands or managed forests is a pervasive problem throughout the Rocky Mountains. Removal of trees from mountainous watersheds increases annual stream discharge and changes runoff regimes (Cheng, 1989; Hauer, 1991). Likewise, the short-term flux of nutrients, particularly phosphorus and nitrogen, increases significantly when watersheds are logged (Hauer and Blum, 1991). These ecosystem-level perturbations have affected aquatic system biodiversity even in headwater drainages (Frissell *et al.*, 1993).

Most large river systems of the Rocky Mountain Region are regulated (i.e. dams, diversions, abstraction). Much of this activity has been concentrated in intermontane valleys where river waters are extracted for crop irrigation and municipal water supplies. In the absence of population centres, high-head hydroelectric dams inundate tens of kilometres of river segments and associated wetlands. Biota dependent on riparian habitats for portions of their life histories are invariably affected. Rivers downstream of dams experience significant change in hydrographs, thermal characteristics and alteration of zoobenthic and fish populations (Stanford and Hauer, 1992). Although most dams are located in intermontane valleys, there is increasing interest in micro-hydroelectric generation in headwater areas.

Introduction of non-native fish, invertebrates and macrophytes is widespread in Rocky Mountain freshwater ecosystems. Over 95% of mountain lakes are naturally fishless, yet >55% of the >16 000 US lakes have been stocked (Bahls, 1992; Donald, 1987). In alpine lakes, introduced trout rapidly eliminate large-bodied invertebrates that dominate food-webs (e.g. Anderson, 1972; Anderson and Donald, 1978) and biogeochemical cycles (Leavitt *et al.*, 1994). In many cases, stocked fish die out (Donald, 1987), yet invertebrate communities are slow to recover (Anderson and Donald, 1978; Paul and Schindler, 1994). The high variability in recovery rates between lakes may obscure our ability to detect lake response to climatic change. Mountain lakes that historically contained fish have also been damaged by indiscriminate stocking practices of non-native species and occasional poisoning with non-specific toxins (rotenone, toxaphene) to eliminate 'undesirable' native fish (Miskimmin *et al.*, 1994).

The long-term effects of global change are likely to exacerbate the effects of direct anthropogenic factors that are already detrimental to stream salmonids. For example, all the native species of salmonids, including six endemic subspecies of cutthroat trout, have declined during the last century (Behnke, 1992; Young, 1995). Most are either already listed as threatened under the US Endangered Species Act or are candidates for such a listing. Numerous large, valley bottom lakes (e.g. Flathead, Whitefish, Pend Oreille) inhabited by adfluvial species (e.g. cutthroat trout, bull char) have been further disrupted by introductions of *Mysis relicta*, an invertebrate predator that has decimated zooplankton populations and significantly altered the food-web dynamics (e.g. Spencer *et al.*, 1991). Many salmonid populations are becoming endangered, a problem that will most likely be exacerbated by projected climate change.

The Rocky Mountain Region has experienced rapid human population growth over the past two decades. While the very largest population centres have grown along the piedmont of the east slope (e.g. Calgary, Denver), municipalities in the intermontane valleys have seen explosive growth in the past decade. Rapid population growth often depletes freshwater resources as municipalities use nearby rivers and lakes for domestic water supplies and downstream waters as the recipient of municipal sewage.

RECOMMENDATIONS

Atmospheric increase in greenhouse gases (e.g. CO_2, CH_4, N_2O, CFCs) during the past century, and particularly since 1950, are well documented (reviewed in Levine, 1992). A World Meteorological Organization (1985) study concluded that the predicted equilibrium surface warming as a consequence of these increases for the period 1980–2030 ranges from 0·8 to 4·1°C. However, adequately predicting the effects of climate change at the regional level has been particularly problematic. Global variables affecting climate range from being easily measured (e.g. atmospheric increase in CO_2) to being very difficult to measure (e.g. thermal response of deep ocean currents to solar radiation). Coupling models of ocean response to increased concentration of greenhouse gases and atmospheric response variables at a global scale have proven to be particularly difficult. Likewise, global climate models have not been dynamically linked to regional climate or hydrological models. Although freshwater ecologists have speculated as to the potential consequences of global warming and the subsequent change in global climate, they have been limited on several areas of study; partly because of the fundamental problems of predicting climate change and partly because biological systems do not always respond as anticipated. In spite of these limitations, strong ecological inferences have been forthcoming, including formalization of our current understanding and identification of critical areas of uncertainty that require further investigation.

Both long-term (monitoring) and short-term (experimental) interdisciplinary studies are needed to resolve what remain as critical uncertainties in our understanding of climate change at the regional and local spatial scale and the response variables that underpin freshwater ecosystem integrity (*sensu* Angermeier and Karr, 1994). Research is needed to make accurate predictions of consequences regarding climate change and freshwater ecosystem response; and, as importantly, to formulate informed and appropriate management responses. This research should be conducted at the watershed (catchment) scale within an organizational framework of research nodes of at least 3–4 locales along the Rocky Mountains extending from northern Canada through Montana to Colorado. Two such research nodes are currently conducting watershed-level research specifically focusing on freshwater response to climate change; McDonald Basin, Glacier National Park in Montana, and Loch Vail in Colorado. Similar research nodes should be established in a far northern locale (e.g. Jasper, Canada) and in a central Rockies locale (e.g. Wyoming). Research nodes should be programmatically linked to coordinate methods, databases and information exchange.

Long-term, time-series data need to be systematically collected at research nodes to establish firmly the baseline data of thermal regimes, radiant energy flux, precipitation, hydrology, biogeochemical fluxes and an inventory of biological populations. These data should include remotely sensed areal features such as snow cover, lake optical properties, vegetation and land use. Short-term, experimental studies in the field and laboratory are needed to establish firmly the role of climatic drivers and the response variables of the aquatic ecosystems at different levels of temporal and spatial organization (*sensu* Minshall, 1988). For example, we need to understand, at the biogeochemical level, the source, fate and flux rates of nutrients that control bioproduction, at the species level, the bioenergetics of dominant or keystone species in an array of lake and stream types to determine species-specific response to thermal regimes; at the population level, the dynamics and the effects of habitat fragmentation on metapopulations; and, at the community level, the interactions between temperature and biotic interactions (e.g. competitive exclusion of cutthroat trout by brook trout at higher temperatures). Finally, palaeoecological studies are needed, using glacial geomorphometry, pigments, invertebrate remains, pollen, macro-fossils and geochemistry, to understand past responses of aquatic systems to warming since the 'Little Ice Age' (*ca.* 150–300 BP) and the 'Younger Dryas' (*ca.* 12 000 BP).

Although freshwater ecosystems in the Rocky Mountains have received anthropogenic effects over the past century, near-pristine conditions exist in many hydrologically and geographically diverse drainages throughout the region. Many of the continent's premiere parks (e.g. Jasper, Waterton-Glacier, Yellowstone, Rocky Mountain) and wilderness areas (e.g. Bob Marshall, Frank Church), as well as many of the headwaters of the continent's large river systems, are distributed along the Rocky Mountain spine. The Rockies contain some of the least altered freshwaters among temporate regions of the world. High elevation waters generally have few dissolved ions, poor buffering capacity and relatively simple communities and trophic structures. The biogeochemistry, biological production, food-web dynamics and biogeography of montane lakes, streams and wetlands are greatly influenced by snowpack depth, rate of snowmelt and thermal budget; each of which are directly affected by the climate. Thus, the many pristine aquatic systems distributed across well-defined climatic and elevational gradients throughout the Rocky Mountains may also be among our most sensitive indicators of global climate change and confer important implications for the suitability of the region as a global indicator of change and the effects on aquatic ecosystems. Furthermore, because freshwater resources are fundamental to the human economy, as well as to biodiversity, it is critical that we come to an understanding of the interrelationships of climate change and freshwater ecosystem change in this critically important region.

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Dams and Downstream Aquatic Biodiversity: Potential Food Web Consequences of Hydrologic and Geomorphic Change

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ABSTRACT / Responses of rivers and river ecosystems to dams are complex and varied, as they depend on local sediment supplies, geomorphic constraints, climate, dam structure and operation, and key attributes of the biota. Therefore, "one-size-fits-all" prescriptions cannot substitute for local knowledge in developing prescriptions for dam structure and operation to protect local biodiversity. One general principle is self-evident: that biodiversity is best protected in rivers where physical regimes are the most natural. A sufficiently natural regime of flow variation is particularly crucial for river biota and food webs. We review our research and that of others to illustrate the ecological importance of alternating periods of low and high flow, of periodic bed scour, and of floodplain inundation and dewatering. These fluctuations regulate both the life cycles of river biota and species interactions in the food webs that sustain them. Even if the focus of biodiversity conservation efforts is on a target species rather than whole ecosystems, a food web perspective is necessary, because populations of any species depend critically on how their resources, prey, and potential predators also respond to environmental change. In regulated rivers, managers must determine how the frequency, magnitude, and timing of hydrologic events interact to constrain or support species and food webs. Simple ecological modeling, tailored to local systems, may provide a framework and some insight into explaining ecosystem response to dams and should give direction to mitigation efforts.

Some effects of dams on rivers and their biota are immediate and obvious, but others are gradual and subtle (Petts 1980, Brookes 1994). Brookes (1994) distinguished between first-order impacts that occur shortly after dam closure, and second-order impacts that arise over time due to geomorphic responses of the channel and floodplain to changes in hydrologic and sediment transport regimes. Downstream impacts of dams on river biota due to migration blockage and altered thermal, nutrient, and sediment loading regimes have been extensively documented (e.g., Ward and Stanford 1979, Lillehammer and Saltveit 1984, Petts 1984, Craig and Kemper 1987). These studies have tended to emphasize impacts on species distributions and life histories, rather than ecological interactions (but see Weisberg and Burton 1993). Here, we will focus on how altered flow regimes, such as those that occur downstream from dams, can affect predator–prey interactions in food webs. Dams have obvious hydrologic impacts when they decrease downstream flow variation, and the frequency of bed scouring flows. Channel incision is another widespread, but more gradual, and in some cases more subtle, downstream impact of dams. Its consequence, the reduction or elimination of access for biota to lateral floodplain habitats may also diminish the resilience, productivity, and biodiversity of river ecosystems.

KEY WORDS: Dams; Food webs; Hydrologic disturbance; Predator–prey dynamics; Succession

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Biodiversity in Rivers and Watersheds

"Biodiversity" is a term that is widely used but not yet well defined. It refers to the variety of elements at different levels of biological organization, ranging from genetic through population, community, and ecosystem to landscape levels, that characterize natural ecosystems (Reid and Miller 1989, Noss 1990, Angermeier and Karr 1994). In rivers, for example, biodiversity is diminished if hatchery-raised salmonids are introduced into habitats where different genetic races of the same species evolved. Landscape diversity is particularly important on river floodplains (Sparks 1995), where, for example, differences in elevation can differentiate habitats and refuges for plant and animal species that differ in their requirements for soil moisture or water depth. Biodiversity also connotes a goal to preserve global species diversity. Therefore, biodiversity is seen to increase with the number of native species remaining in an ecosystem, but to diminish when exotic species arrive with deliberate or inadvertent human help (Angermeier 1994) because these can lead to the eventual extinction of local species. Dams, then, reduce biodiversity if they exterminate native species or threaten to push these populations towards extinction by facilitating invasions of exotic species or altering the physical habitat.

Food chain length is one indicator of biodiversity (Reid and Miller 1989, Angermeier and Karr 1994). Food webs are complicated by features such as omnivory, but often chains of energy flow and of strong interactions link certain predators through intermediate consumers to plants or other resources (Paine 1980, Power 1990, 1992a). Chain length (the number of trophic levels in a chain) can be counted by descriptive bottom-up criteria, based on the number of energy transfers inferred from diet analyses (e.g., Cohen 1978) or isotopic fractionation (e.g., Kling and others 1992, Cabana and Rasmussen 1995). Alternatively, the length of functionally significant food chains can be counted by top-down criteria as the number of guilds or populations that are alternately released and suppressed following removal of a top predator. In general, counts of functional trophic levels in food chains, which require potential population regulation (Fretwell 1977, Oksanen and others 1981, Power 1992a), will differ in length from descriptive counts based on energy transfers. For example, juvenile steelhead and large roach (cyprinids) in the Eel River of northern California occurred at the fourth trophic level in functional food chains where experimental manipulations showed that they suppressed small predators, releasing an algivorous midge that was invulnerable to the larger fish, which in turn grazed down algae (Power 1990). Descriptive diet analyses would have placed these larger fish at the third trophic level, however, as algivorous mayflies were the predominant prey found in their guts (Power and others 1992).

Longer functional food chains often occur in more pristine (and desirable) river communities. We will introduce this view with an extreme but not unrealistic example. In arid watersheds in the southwestern United States, water abstraction and overgrazing have virtually eliminated aquatic and riparian vegetation. Nitrogen oxides from polluted air rain down on, but are not taken up by, plants. Instead, they make their way into the groundwater. Near Phoenix, Arizona, these circumstances have led to water wells being shut down because they have accumulated toxic levels of nitrates. According to stream ecologists Stuart Fisher and Nancy Grimm from Arizona State University, residents in the region are literally drinking their own automobile exhaust (personal communication and Koppes 1990). This scenario depicts a river–watershed ecosystem with zero functionally significant trophic levels, i.e., no plants capable of regulating their nitrogen resources. Add plants (one trophic level), and the wells may stay open, but eutrophication problems arise if macrophyte or algal accrual is considered excessive. Add grazers (two trophic levels), and plants may be regulated, but pestiferous outbreaks of insects may occur. Add predatory invertebrates and small fish (three trophic levels) and the situation improves; if these feed larger fish, birds, and wildlife, human anglers, sportsmen, hikers, and naturalists are generally happier. In general, the quality of natural environments for humans increases as food chains lengthen. Values inherent in the notion of biodiversity often correlate positively with the length of functional food chains, unless longer food chains result from the introduction of exotic predators (such as bullfrogs in western US rivers, or Nile perch in Lake Victoria).

Much remains to be learned about how functional food chain length responds to changes in the physical environment. There is presently no secure general theory for predicting the length of descriptive or functional food chains in natural ecosystems. The two most studied hypotheses predict that (1) food chains should lengthen with environmental productivity or the metabolic efficiency of consumers (Elton 1927, Slobodkin 1961), and (2) food chains should shorten with environmental disturbance (Pimm 1982, Pimm and Lawton 1977). While these two hypotheses have been considered as alternatives, it is obvious that disturbance and productivity regimes might interact to influence food chain length.

Food Chain Hypotheses
(1) Length ↑ P
(2) Length ↓ D
(3) Length ↔ P + D

Effects of Flow Variation on Food Chain Length

Surveys and experiments during drought and flood years in northern California rivers suggest that the lengths of functionally important food chains in rivers generally increase with natural regimes of flow variation. These regimes include bed-scouring floods that qualify as ecological disturbances, because they impose huge mortality on substrate-bound biota. Mechanisms for this result, which does not support the theoretical prediction that disturbance should shorten food chains, involve familiar life history trade-offs between resilience following physical disturbance and resistance to predators for early versus late successional species at lower trophic levels (see Scouring Flows and Succession, below). Flow variation also gives riverine predators periodic access to their prey, while preventing them from overharvesting. In small or incised rivers, prey may enjoy respite from predation during periods of low flow, when shallow in-channel habitats block access for larger predators (see Flow Variation and Predator–Prey Interactions, below). The converse may apply in larger floodplain rivers, where predation may be most intense during low flow periods when predators and prey are concentrated together in channels and permanent off-river waterbodies (Lowe-McConnell 1964). In these systems, prey (including young life stages of cannibalistic predators) may require periodic access to inundated floodplains during high flow periods to rebuild their populations (see Inundation and Dewatering of River Floodplains, below). We will briefly review several case studies from our research and that of others to illustrate these interactions of flow variation with food chain length.

Flow Variation and Predator–Prey Interactions

Brier Creek, in south central Oklahoma, is a small incised stream. During low-flow periods, pools are well isolated from each other by long shallow riffles. Some pools are filled with filamentous green algae (predominantly *Rhizoclonium*), while others are barren. Green pools contain bass (*Micropterus salmoides* and *M. punctatus*); barren pools lack bass and contain schools of the grazing minnow, *Campostoma anomalum*, which are absent in bass pools. Redistribution of bass and *Campostoma* among pools, by floods or experimentalists, can change green bass pools to barren *Campostoma* pools (from three to two trophic levels) within weeks. Dynamics in the opposite direction are equally rapid (Power and others 1985). When bass are added to *Campostoma* pools, some minnows are eaten, but others (in some trials, up to half of the original population) emigrate to avoid bass. Minnows cross shallow riffles to swim to bass-free pools (Power and others 1985). At low flow, bass are too deep-bodied to follow them. If flows were chronically low, bass trapped in pools without minnows would starve. If flows in Brier Creek were chronically high enough so that riffles were corridors rather than barriers for bass, bass might overeat their minnow prey throughout the entire stream and then starve. Methods that only evaluated habitat availability for particular taxa [e.g., instream flow incremental methodology (IFIM) models (Orth and Maugham 1982, 1986)] would not predict or explain population declines for bass or minnows if these arose due to the lack of the variable flow regimes required to sustain the predator–prey dynamics.

IFIM critique

Inundation and Dewatering of River Floodplains

In larger, lowland rivers, floodplain habitats are extremely important as feeding areas, nurseries, and overwintering habitats for riverine fishes and other biota (Welcomme 1985, Bayley 1995, Sparks 1995, Junk and others 1989). Reduced access to floodplains can greatly diminish the productivity and, in some cases, the viability of these populations (Sparks and others 1990).

River floodplains are spatially, hydrologically, and biologically complex and dynamic (Junk and others 1989, Welcomme 1985). Ecologists have long recognized that spatial heterogeneity and temporal fluctuation can play strong roles in maintaining the richness and complexity of ecological communities. In heterogeneous, fluctuating environments, consumers are less likely to overeat and exterminate their prey (Hastings 1977, Huffaker 1958). Competitors that dominate under particular conditions are likely to lose their performance advantage before they can exclude lesser competitors (Connell 1978, Hutchinson 1961, Tilman 1994). Therefore, the hydrologic fluctuations that impose huge stranding mortality on river biota (Bonnetto, cited in Welcomme 1985) may, paradoxically, enhance the persistence of ecological communities by reducing the chances that their constituent populations will go extinct (Sparks 1992, Welcomme 1985). These views are supported by our preliminary simulation studies of simplified floodplain river food chains. In hydraulic food chain models, river food chains could sustain top predators only when the river biota had periodic access to floodplains. When flow diversions or levees prevented spillover, only two, or in some simulations one, trophic level(s) persisted (Power and others 1995a).

env. gradient

Hydraulic food chains constitute a modeling approach that links the relatively well understood responses of river width, depth, and velocity to changes in discharge to the poorly understood responses of river biota to these hydraulic parameters (Power and others 1995a,b). The food webs are modeled as modified Lotka-Volterra equations for food chains with three or four trophic levels and two energy sources, detritus and vegetation. Strengths of interaction between or among trophic levels are modulated by hydrologic changes in two ways. First, mobile or drifting components of the food web are concentrated within the channel during low flow and diluted over floodplains when these are inundated after spillover. Second, certain biological parameters (e.g., growth, feeding, or mortality rates) in the coupled biomass balance equations are written as explicit functions of hydraulic variables (flow width, depth, velocity, or interactions of these terms). These hydraulic food chain models are not intended as predictive tools, but as conceptual frameworks to guide field observations and measurements when tailored to specific ecosystems.

Scouring Flows and Succession

As mentioned above, our surveys and experiments suggest that, in contrast to the theoretical prediction that disturbance should lead to shorter food chains, bed scouring floods can lengthen functionally important food chains in northern California rivers. In California's Mediterranean climate regime, rivers normally experience flooding during winter months and a period of low flow during summer. After scouring floods, primary consumer (grazer) guilds in northern California rivers are initially dominated by mobile, unarmored (e.g., mayfly nymphs) or lightly armored invertebrate taxa. Over time, these early successional taxa, which are vulnerable to predators, are replaced by more heavily armored or sessile forms that are less vulnerable. Allocations to defense (armor, silk for retreats, and/or a sessile life-style) rather than to protoplasm and offspring slow the somatic and population growth as a population rebounds from flood scour, but such traits confer immunity from predators in our system. Consequently, defended late successional taxa come to dominate grazer guilds when flood-free periods last more than one year: during prolonged drought or in channels with artificially regulated flow (Power 1992b, 1995, Power and others 1995c). Selective predation is sufficient to explain these changes, but there is also evidence that sessile (late successional) grazers may outcompete mobile (early successional) taxa (e.g., McAuliffe 1984). Comparisons of these successional trends in a sunny river with higher primary productivity and a darker tributary with lower primary productivity suggest that late-successional, predator resistant taxa may dominate lower trophic levels sooner after disturbance in more productive habitats. An explanation is that these resistant taxa can recover from disturbance and take over space and algal resources more quickly following disturbances if local rates of food renewal are high.

species traits

Glossosoma

Invert succession

algal succession

Succession from more to less edible species following floods can also occur at the first trophic level among primary producers. In Brier Creek, Oklahoma, epilithic diatoms, followed by the green alga *Rhizoclonium*, dominated stream substrates after a flood. Within 26 days, however, *Rhizoclonium* was replaced by the green alga *Spirogyra* at many sites (Power and Stewart 1987). Diatoms are among the most edible and nutritious of algae for stream grazers (e.g., Kupferberg and others 1994). Epilithic diatoms were overgrown by *Rhizoclonium*, but this rough-skinned macro-alga supports high densities of epiphytic diatoms. When epiphytized, *Rhizoclonium* is greatly preferred by grazers to *Spirogyra*, which has a mucousy surface to which diatoms cannot adhere. *Spirogyra*'s ability to slough epiphytes and to grow as floating masses that can shade the rock-bound *Rhizoclonium* allow this less palatable alga to become increasingly dominant during later stages of succession following flood scour (Power and Stewart 1987).

These successional changes in primary producers in Brier Creek and in primary consumers in northern California rivers both imply that energy transfer from lower to higher trophic levels (e.g., fish) may attenuate in the absence of annual flood scour, a prediction we are currently investigating in regulated and unregulated northern California streams. Periodic rejuvenation of the food web supporting fish and other higher trophic levels is one of several reasons to maintain an adequate frequency of bed scouring flows. Another well-documented ecosystem service of flushing flows is the cleansing and resupply of spawning gravels for salmonids (e.g., Mundie 1979, Kondolf and others 1991, 1993, Ligon and others 1995, Milhouse in preparation). In addition, in western US rivers, flushing flows often suppress invading alien riverine species. Many alien animal species that threaten native species in western US rivers today are introductions from more lentic aquatic habitats [e.g., bullfrogs (Hayes and Jennings 1986), large-mouth bass and other piscivorous centrarchids (Moyle 1976, Moyle and others 1986); and mosquitofish (*Gambusia affinis*) (Meffe 1984, Meffe and Minckley 1987)]. These taxa tend to move upstream into steeper parts of watersheds during periods of low flow but are displaced downstream to a much greater degree than are natives during floods (Meffe 1984, Kupferberg 1996, Power and Roberts, unpublished data). In addition, alien plants, such as tamarisk, an aggressive spreader with high rates of evapotranspiration that can severely lower water tables, are also commonly more vulnerable to flood scour than is native vegetation (Stromberg 1993, Stromberg and others 1993, personal observations). Periodic flushing may generally enhance biodiversity by differentially clearing channels of encroaching plant or animal alien species. In some cases, flushing flows also serve to clear native vegetation as well, which, in the prolonged absence of scouring flows, can encroach to an extent that diminishes local biodiversity.

Vegetation Encroachment into Channels

Although riparian and aquatic plants are crucial to the structure and function of ecological communities in streams, reduced flows can allow vegetation to encroach into river channels to an extent that leads to practical problems, such as reduced flood conveyance (Wade 1994), and to ecological concerns. On the Trinity River ref. for BS paper

of northern California, vegetation encroachment downstream from a dam has greatly reduced the cobble bar habitat that yellow-legged frogs (*Rana boylii*) require for oviposition (Lind and others 1996). Another dramatic example comes from the work of South African scientists. The Sabie-Sand River is one of six formerly perennial rivers draining from the west into Kruger National Park (Davies and others 1994). The pools of this bedrock-bedded river are required as habitat for hippopotomi and crocodiles, as well as for surface water used by elephants, giraffes, and other terrestrial megafauna. Upstream from Kruger Park, water abstraction for silviculture (of exotic eucalyptus and pines), commercial agriculture, and drinking water supplies to rural settlements in the former homelands caused the Sabie to stop flowing for the first time in 1989 and again in 1992 (Davies and others 1994). Carter and Rogers (1989) document a worrisome transition in the Sabie within Kruger National Park, from bedrock water pools to sand to reed beds to woody riparian vegetation. This successional sequence involves a positive feedback that makes it difficult to reverse. Reeds (*Phragmites mauritianus*) establish extensive beds when sediments are deposited by low flows. Established reeds trap more sediment and evapotranspire off more water, creating conditions that further enhance their spread until the surface water is gone. Flow releases from two proposed dams that will be built on the Sabie must be extremely carefully planned if they are not to cause serious further degradation to what Davies and others (1994) have called "this major lifeline to the premier wildlife conservation area in South Africa."

Management Considerations and Research Priorities

If dams are to be redesigned and managed to better protect biodiversity, we need to implement our existing understanding and develop better understanding in three areas. Listed in increasing order of their complexity and our uncertainty, these are the geomorphic, ecological, and socioeconomic factors that respond to and constrain dam and river management.

Geomorphic Considerations

As Ligon and others (1995) stated, if the physical foundation of a river's ecosystem is pulled out from under the biota, even the most insightful biological research and management program will fail to preserve biodiversity. Given the limited time, money, and knowledge available for mitigating dam effects of biodiversity, they recommend emphasis on maintaining the dynamic physical regimes that, over the long term, maintain the habitat's essential predam geomorphology. We understand in general how the frequency and magnitude of channel discharge and sediment transport events determine channel and floodplain morphology (e.g., Wolman and Miller 1960, Leopold and others 1964). Challenges remain, however. While dominant discharge concepts in geomorphology recommend the maintenance of predam bankfull flow levels, rarer events may be crucial to generating habitat diversity [e.g., topographic variation on floodplains (Sparks 1995)] essential to the biota. Rare superfloods, for example, may be needed to clear reedbeds from pools of the Sabie River, but geomorphologists may not be able to predict the required frequency and magnitude, because we know too little about flow-through vegetation. In general, site-specific research will be necessary because local geomorphic responses of rivers to dams are varied and complex and depend on sediment supply, local geomorphic constraints, and dam structure and operation. Riverbeds may incise or aggrade, affecting floodplain inundation; bed sediments may coarsen or fine (Williams and Wolman 1984); channel patterns may change (e.g., from braided to single thread) (Stanford and Ward 1993, Ligon and others 1995).

While some physical changes caused by dams are immediate and obvious, others are so gradual that they may go unrecognized by humans using the river for many years and by biological teams focused on local habitat assessment. This may be the case with gradual channel incision downstream from dams (Ligon and others 1995). Causes of downstream incision are well understood. Large dams can trap virtually all of the incoming sediment (Williams and Wolman 1984). Channels downstream are cut off from replenishing supplies of sediment and, as a consequence, commonly degrade (Leopold and others 1964). Channel degradation or incision may persist for tens to hundreds of kilometers downstream from high dams (Williams and Wolman 1984). What may be more difficult to recognize, particularly where incision is subtle and historical topographic surveys are lacking, is that even slight incision of channels may have strong ecological effects. Channel incision will lower water tables around the river, with consequences for riparian vegetation that feed back to affect river communities (e.g., Stromberg 1993, Murphy and Koski 1989). In addition, channel incision will reduce the number and duration of overbank flows, reducing access to floodplains for river biota. Dam-protected human developments on floodplains can make this loss for biodiversity seemingly permanent, but repeated flooding during 1993 and afterwards is causing humans to rethink their land-use practices along rivers like the Mississippi and the Russian River of

California. Floodplain restoration for biodiversity is a particularly promising area for future research in ecological engineering (Sparks 1995, Bain and Boltz 1989).

Channel incision effects could be reduced or possibly prevented by dams designed to periodically pass stored sediments. This feature would have also great practical importance, as it would maintain the upstream water-storage capacity of reservoirs. Engineering research is needed here, as regular passage of sediment is presently feasible only for relatively small reservoirs (Ligon and others 1995). Alternatively, perhaps this consideration should constrain the size of future dams that are built.

Ecological Considerations

Previously, ecological impacts of regulated flow regimes have been largely assessed by evaluating their effect on the availability of habitat units within certain ranges of physical parameters (e.g., depth, velocity). These methods, of which the instream flow incremental method (IFIM) is the best known, point out the linkage between flow regulation, physical habitat availability, and fish (Orth and Maughan 1982, 1986) or invertebrates (Gore and others 1989). While these methods provide information of value linking land use to habitat dynamics of focal species, they are not sufficient because they ignore vital ecological linkages, such as those among focal species and their food or predators (e.g., Mathur and others 1985). Even if the focus of biodiversity conservation efforts is on a target species rather than whole ecosystems, a food web perspective is necessary, because the population dynamics of any species depend critically on how their resources, prey, and potential predators also respond to environmental change (e.g., Weisberg and Burton 1993). In addition, these methods are too "close-focus," time-consuming, and costly to apply when practical problems require a larger-scale, more holistic overview (King and Tharme 1993, cited in Davies and others 1994).

To conserve native species, we must understand how flow regimes influence the key interactions in the food webs supporting them. Our hydraulic food chain models (Power and others 1995a,b) are examples of such approaches, although our efforts are still quite preliminary. Such approaches should be more macroscopic than IFIM assessments. To apply such methods, we would first determine the large-scale geomorphic features of a river system that affect how water and sediment are routed through it (average downstream slope, whether the bed is alluvial or bedrock, pool frequency and volume, bankfull depths, positions of major tributaries, etc.). Next, we would construct an interaction web representing our best guess at the crucial ecological processes that regulate abundances of focal species. These species may be singled out for attention because they are strong interactors in food webs (Paine 1980), because they are threatened or endangered, or because they have commercial or cultural value (e.g., Ligon and others 1995). We would attempt to determine and model those life history stages that are bottlenecks for these species. Expert systems models that interrogate people with knowledge of local ecology may be useful at this stage (O'Keefe and Davies 1991, Starfield and others 1989). When interaction webs have been drawn up, they should be trimmed to be as parsimonious as possible (representing only interactions hypothesized to be crucial). At this stage, we would consider how channel hydraulics and hydrology, under various flow regimes, would influence the key species interactions represented. In our hydraulic food chain approach (as described above), these influences are mediated both by the dilution and concentration of biota as river stage rises and falls and by the effects of discharge-related parameters (flow velocity, depth, width, or derived variables such as turbidity) on the rates of ecological processes (birth, growth, mortality, feeding, movements, etc.). The model at this stage should motivate focused field work to calibrate relationships that appear poorly defined but important. Once partially calibrated, the model may (tentatively) suggest how to manage flow regimes to preserve the ecological functions needed to sustain species and food webs. An adaptive management approach (Walters 1986) should be adopted that treats the model predictions and recommendations as hypotheses. The actual behavior of the system under specified managed flow regimes should be closely monitored, and data and insights from this monitoring program should feed back to improve the model that motivates the management. This iteration should be prolonged.

Models that address the ecological effects of flow and sediment transport must consider the timing of major events as well as their frequency and magnitude. The required regimes may involve periodically deepening riffles between pools so predators have access (but not continual access) to prey (e.g., Brier Creek); periodically inundating floodplains long enough so that prey populations and young life history stages have sufficient time to grow in numbers or body size before they lose these refuges from predators after reconfinement of floodplain rivers, and periodically stirring the beds of gravel-bedded rivers so that early successional prey taxa can rejuvenate food chains, facilitating the flow of energy to higher trophic levels (e.g., northern California rivers). In many situations, there will be magnitude–frequency trade-offs for managers to consider. For example, the longer the interval between flows that scour out vegetation encroaching downstream from dams, the larger will be the magnitude of the discharge required to uproot larger, denser, better established vegetation.

Above, we have stressed the importance of providing some minimum frequency of flow variation in regulated rivers, but commonly flow variation is too frequent for the biology. Effects on invertebrates and fish of hydroelectric power-peaking regimes that fluctuate with artificially high frequencies have been reviewed by Gore (1994). If flood pulses can be delivered with more natural frequencies, the timing of flow releases can be managed to benefit, rather than harm, biodiversity. Potamodromous fish in the Zambezi River were able to spawn downstream from Kariba dam, provided that peak flows were discharged during the correct season (Kenmuir 1976, cited in Davies 1979). Managers can also time flow releases to favor native species and disfavor alien invaders. For example, in western US rivers, scouring flows should not be released when vulnerable life history stages of salmonids or native frogs (eggs, larvae) are present (Lind and others 1996). In some cases, however, spring or summer pulses might be useful as a management strategy, e.g., to flush out alien bullfrog eggs or to discourage invasive alien vegetation. Determining what range of flow conditions is acceptable for life stages and species of special concern and how capable species are of tracking these conditions within watersheds should also be priority for research. Kupferberg's (1996) study of how the geomorphic characteristics of oviposition sites of foothills yellow-legged frogs (*Rana boylii*) affect the survivorship of their egg masses during spring runoff exemplifies the type of study needed to understand how physical regimes in natural and altered rivers will affect species population dynamics. Simple modeling approaches, like our hydraulic food chain models, can organize our thinking about the relevant time scales for these processes and interactions and suggest which areas of uncertainty (about interactions, relationships or parameter values) would be most useful to further investigate.

BS ref.

Socioeconomic Considerations

Although there are practical benefits for some of the management goals outlined above, in general they will not be cheap to implement. As the electric power industry experiences deregulation, pressures increase to produce energy as cheaply as possible. Deregulation, however, may also give local utilities increased access to a growing national market marked by "green consumerism." If environmental scientists and dam managers can comprehend and clarify how managed and natural flow regimes affect river ecosystems in a sufficiently timely fashion, utilities will be in a position to inform their customers and stockholders when specific decisions arise that require trade-offs between production efficiency and environmental protection. If such choices are made clear and explicit, utilities may discover, and help to expand, a viable national market that can support energy produced in an environmentally sound manner.

Vaclav Havel, in his 1990 New Year's address to the Czech people as their newly elected president, commented that they had inherited ". . . the most contaminated environment in Europe," in part because "The previous regime—armed with its arrogant and intolerant ideology—reduced man to a force of production, and nature to a tool of production" (Havel 1995). He was speaking, of course, of the previous communist totalitarian regime that ruled Czechoslovakia. It remains to be seen whether a democracy, with an economy that currently is increasingly structured by free market forces, will, in the long run, do better.

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Uncertainty, Resource Exploitation, and Conservation: Lessons from History

-based on E.M.-- Ecol. integrity -

Donald Ludwig, Ray Hilborn, Carl Walters

sustainability -fact/fiction

There are currently many plans for sustainable use or sustainable development that are founded upon scientific information and consensus. Such ideas reflect ignorance of the history of resource exploitation and misunderstanding of the possibility of achieving scientific consensus concerning resources and the environment. Although there is considerable variation in detail, there is remarkable consistency in the history of resource exploitation: resources are inevitably overexploited, often to the point of collapse or extinction. We suggest that such consistency is due to the following common features: (i) Wealth or the prospect of wealth generates political and social power that is used to promote unlimited exploitation of resources. (ii) Scientific understanding and consensus is hampered by the lack of controls and replicates, so that each new problem involves learning about a new system. (iii) The complexity of the underlying biological and physical systems precludes a reductionist approach to management. Optimum levels of exploitation must be determined by trial and error. (iv) Large levels of natural variability mask the effects of overexploitation. Initial overexploitation is not detectable until it is severe and often irreversible.

In such circumstances, assigning causes to past events is problematical, future events cannot be predicted, and even well-meaning attempts to exploit responsibly may lead to disastrous consequences. Legislation concerning the environment often requires environmental or economic impact assessment before action is taken. Such impact assessment is supposed to be based upon scientific consensus. For the reasons given above, such consensus is seldom achieved, even after collapse of the resource.

For some years the concept of maximum sustained yield (MSY) guided efforts at fisheries management. There is now widespread agreement that this concept was unfortunate. Larkin (*1*) concluded that fisheries scientists have been unable to control the technique, distribution, and amount of fishing effort. The consequence has been the elimination of some substocks, such as herring, cod, ocean perch, salmon, and lake trout. He concluded that an MSY based upon the analysis of the historic statistics of a fishery is not attainable on a sustained basis. Support for Larkin's view is provided by a number of reviews of the history of fisheries (*2*). Few fisheries exhibit steady abundance (*3*).

It is more appropriate to think of resources as managing humans than the converse: the larger and the more immediate are prospects for gain, the greater the political power that is used to facilitate unlimited exploitation. The classic illustrations are gold rushes. Where large and immediate gains are in prospect, politicians and governments tend to ally themselves with special interest groups in order to facilitate the exploitation. Forests throughout the world have been destroyed by wasteful and shortsighted forestry practices. In many cases, governments eventually subsidize the export of forest products in order to delay the unemployment that results when local timber supplies run out or become uneconomic to harvest and process (*4*). These practices lead to rapid mining of old-growth forests; they imply that timber supplies must inevitably decrease in the future.

Harvesting of irregular or fluctuating resources is subject to a ratchet effect (*3*): during relatively stable periods, harvesting rates tend to stabilize at positions predicted by steady-state bioeconomic theory. Such levels are often excessive. Then a sequence of good years encourages additional investment in vessels or processing capacity. When conditions return to normal or below normal, the industry appeals to the government for help; often substantial investments and many jobs are at stake. The governmental response typically is direct or indirect subsidies. These may be thought of initially as temporary, but their effect is to encourage overharvesting. The ratchet effect is caused by the lack of inhibition on investments during good periods, but strong pressure not to disinvest during poor periods. The long-term outcome is a heavily subsidized industry that overharvests the resource.

The history of harvests of Pacific salmon provides an interesting contrast to the usual bleak picture. Pacific salmon harvests rose rapidly in the first part of this century as markets were developed and technology improved, but most stocks were eventually overexploited, and many were lost as a result of overharvesting, dams, and habitat loss. However, in the past 30 years more fish have been allowed to spawn and high seas interception has been reduced, allowing for better stock management. Oceanographic conditions appear to have been favorable: Alaska has produced record catches of salmon and British Columbia has had record returns of its most valuable species (*5*).

We propose that we shall never attain scientific consensus concerning the systems that are being exploited. There have been a number of spectacular failures to exploit resources sustainably, but to date there is no agreement about the causes of these failures. Radovitch (*6*) reviewed the case of the California sardine and pointed out that early in the history of exploitation scientists from the (then) California Division of Fish and Game issued warnings that the commercial exploitation of the fishery could not increase without limits and recommended that an annual sardine quota be established to keep the population from being overfished. This recommendation was opposed by the fishing industry, which was able to identify scientists who would state that it was virtually impossible to overfish a pelagic species. The debate persists today.

After the collapse of the Pacific sardine, the Peruvian anchoveta was targeted as a source of fish meal for cattle feed. The result was the most spectacular collapse in the history of fisheries exploitation: the yield decreased from a high of 10 million metric tons to near zero in a few years. The stock, the collapse, and the associated oceanographic events have been the subject of extensive study, both before and after the event. There remains no general agreement about the relative importance of El Niño events and continued exploitation as causes of collapse in this fishery (*7*).

The great difficulty in achieving consensus concerning past events and a fortiori in prediction of future events is that controlled and replicated experiments are impossible to perform in large-scale systems. Therefore there is ample scope for differing interpretations. There are great obstacles to any sort of experimental approach to management because experiments involve reduction in yield (at least for the short term) without any guarantee of increased yields in the future (*8*). Even in the case of Pacific salmon stocks that have been extensively monitored for many years, one cannot assert with any confidence that present levels of exploitation are anywhere near optimal because the requisite experiments would

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(*Continued from page 17*)

involve short-term losses for the industry (*9*). The impossibility of estimating the sustained yield without reducing fishing effort can be demonstrated from statistical arguments (*10*). These results suggest that sustainable exploitation cannot be achieved without first overexploiting the resource.

The difficulties that have been experienced in understanding and prediction in fisheries are compounded for the even larger scales involved in understanding and predicting phenomena of major concern, such as global warming and other possible atmospheric changes. Some of the time scales involved are so long that observational studies are unlikely to provide timely indications of required actions or the consequences of failing to take remedial measures.

Scientific certainty and consensus in itself would not prevent overexploitation and destruction of resources. Many practices continue even in cases where there is abundant scientific evidence that they are ultimately destructive. An outstanding example is the use of irrigation in arid lands. Approximately 3000 years ago in Sumer, the once highly productive wheat crop had to be replaced by barley because barley was more salt-resistant. The salty soil was the result of irrigation (*11*). E. W. Hilgard pointed out in 1899 that the consequences of planned irrigation in California would be similar (*12*). His warnings were not heeded (*13*). Thus 3000 years of experience and a good scientific understanding of the phenomena, their causes, and the appropriate prophylactic measures are not sufficient to prevent the misuse and consequent destruction of resources.

Some Principles of Effective Management

Our lack of understanding and inability to predict mandate a much more cautious approach to resource exploitation than is the norm. Here are some suggestions for management.

1) Include human motivation and responses as part of the system to be studied and managed. The shortsightedness and greed of humans underlie difficulties in management of resources, although the difficulties may manifest themselves as biological problems of the stock under exploitation (*2*).

2) Act before scientific consensus is achieved. We do not require any additional scientific studies before taking action to curb human activities that effect global warming, ozone depletion, pollution, and depletion of fossil fuels. Calls for additional research may be mere delaying tactics (*14*).

3) Rely on scientists to recognize problems, but not to remedy them. The judgment of scientists is often heavily influenced by their training in their respective disciplines, but the most important issues involving resources and the environment involve interactions whose understanding must involve many disciplines. Scientists and their judgments are subject to political pressure (*15*).

4) Distrust claims of sustainability. Because past resource exploitation has seldom been sustainable, any new plan that involves claims of sustainability should be suspect. One should inquire how the difficulties that have been encountered in past resource exploitation are to be overcome. The work of the Brundland Commission (*16*) suffers from continual references to sustainability that is to be achieved in an unspecified way. Recently some of the world's leading ecologists have claimed that the key to a sustainable biosphere is research on a long list of standard research topics in ecology (*17*). Such a claim that basic research will (in an unspecified way) lead to sustainable use of resources in the face of a growing human population may lead to a false complacency: instead of addressing the problems of population growth and excessive use of resources, we may avoid such difficult issues by spending money on basic ecological research.

5) Confront uncertainty. Once we free ourselves from the illusion that science or technology (if lavishly funded) can provide a solution to resource or conservation problems, appropriate action becomes possible. Effective policies are possible under conditions of uncertainty, but they must take uncertainty into account. There is a well-developed theory of decision-making under uncertainty (*18*). In the present context, theoretical niceties are not required. Most principles of decision-making under uncertainty are simply common sense. We must consider a variety of plausible hypotheses about the world; consider a variety of possible strategies; favor actions that are robust to uncertainties; hedge; favor actions that are informative; probe and experiment; monitor results; update assessments and modify policy accordingly; and favor actions that are reversible.

Political leaders at levels ranging from world summits to local communities base their policies upon a misguided view of the dynamics of resource exploitation. Scientists have been active in pointing out environmental degradation and consequent hazards to human life, and possibly to life as we know it on Earth. But by and large the scientific community has helped to perpetuate the illusion of sustainable development through scientific and technological progress. Resource problems are not really environmental problems: They are human problems that we have created at many times and in many places, under a variety of political, social, and economic systems (*19*).

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Commentary

Scientific Responsibility and Responsible Ecology

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Ecology has been called the relevant science. If this relevance is to be anything other than a catchy phrase, two things are necessary. First, ecology must generate reliable information and insights about environmental systems. This means that the information must be gathered in a rigorous and unbiased way and interpreted objectively: the science must be sound. Second, ecological information must be incorporated into management practices and policy decisions, the arenas where this information can make a difference. This means that the information must be gathered in a way that will provide useful insights to management and policy, and it must be communicated in a way that is understandable to people who have not been raised on a diet of ecological jargon.

Baskerville's essay ("Advocacy, science, policy, and life in the real world," *Conservation Ecology*) addresses primarily the second point. Here, I will comment on the issue of scale as it relates to Baskerville's thesis and then offer some thoughts on the first point, which I believe is the more important of the two.

Baskerville notes that the scale on which ecological research is conducted rarely matches the scale of management. In his view, this leads to a preoccupation with describing fine-scale patterns rather than discovering how systems actually function. The latter concern is simply a misreading of current trends and activities in ecology, which are increasingly focused on ecological mechanisms and processes. The concern with mismatched scales, however, is very real, and it permeates all of ecology, whether basic or applied. We know that ecological processes, and the patterns they produce, change as the scale in space or time changes. We also know that these changes are often nonlinear (Wiens 1989, Levin 1992). What we do not know is the nature of the "scaling functions" that describe these relationships for particular phenomena. Thus, although logistical necessity and ecological tradition (e.g., a preoccupation with experiments) usually dictate that ecological investigations be conducted at relatively fine scales of space and time, it is not clear how these findings should be extrapolated to the broader scales on which management is usually practiced. Simple linear extrapolations usually will not work. The issue of extrapolation is one of the most vexing in ecology, but if ecologists wish to contribute to effective resource management and scientifically based policy, it must become a central focus of ecological research. Some progress might be made by implementing carefully designed multiscale investigations (e.g., Koch et al. 1995), by integrating some of the approaches of macroecology (Brown 1995) with fine-scale, mechanistic studies, or by using theories of self-organizing processes in ecosystems (e.g., Holling et al. 1996) as a framework for evaluating scale dependency and scaling functions.

Baskerville argues that, if ecological information is to be relevant to management and policy, ecologists must scale their studies to match the scales used in management. In my view, this is an unrealistic demand, not because ecologists are unlikely to do this, but because it is not likely to advance ecologically based resource management. Management scales have been determined by a variety of factors: some economical, some political, some simply traditional, but all essentially anthropocentric. These scales of management do not necessarily coincide with the scales on which organisms respond to their environments, on which the processes affecting biodiversity or disturbance regimes operate, or on which ecosystems function. Ultimately, the health and profitability of the resources that are being managed depend on these organismal, population, and ecosystem scaling relationships, and to regard the scales of management as fixed and inviolate is a good point

mistake. Rather than imposing a management scale on nature, efforts should be made to adjust the scales of management to those of natural processes, insofar as economic, social, and political constraints permit. This is, in fact, the approach being developed in the "new forestry" practiced in parts of Sweden and elsewhere (Haila 1994, Pastor et al. 1996).

Thus, problems with incorporating ecology into management and conservation stem, at least in part, from problems in translating patterns and mechanisms across scales. Detecting such scale-dependent effects depends, of course, on the scientific rigor of the studies conducted. More importantly, how (or whether) ecological science is applied to broader issues of public concern depends critically on the integrity of the scientific process. Let me turn now to the issue of sound science.

Ecologists are increasingly being drawn into environmental debates, whether about the effects of land uses or management practices (such as grazing of rangelands or clearcutting of forests), conservation issues (such as the design of natural reserves or the management of endangered species), or environmental perturbations (such as oil spills or global change). These are often emotionally charged issues. They attract media attention and, not infrequently, foster litigation. Because they are socially relevant, they are often associated with opportunities for research funding. Collectively, these pressures create an atmosphere in which advocacy for a particular position in a debate may affect the scientific process. At its worst, advocacy may masquerade as science (Wiens 1996) or science may be perceived as advocacy (Westoby 1997). Both erode the credibility of honest science.

Advocacy can influence the scientific process in several ways, beginning with the questions we ask. Most questions in ecology are influenced by our preconceptions about nature or current fashions in the discipline. Questions that relate to environmental or management issues often carry with them values (e.g., oil spills are bad) that can affect the way the questions are framed and the range of answers that can be obtained. Thus, instead of asking, "Did an oil spill have environmental effects, and if so, what?", the question may become "How bad were the effects?" The distinction is important, for the first question leads to an unbiased examination of environmental effects, whereas the second restricts attention only to environmental damages. We often initiate a study because of some environmental debate and the need to bring scientific evidence to bear on the issues, so some element of advocacy in the questions we ask is probably unavoidable. Biased questions, however, do not lead to good science.

Advocacy can also affect the way a study is designed. It can lead to conscious or unconscious bias in the selection of study areas, the way sampling stations are distributed, or the degree to which pseudoreplication is tolerated. Control areas may differ systematically from treatment areas, for example, but these differences may be ignored in analyzing results; as a consequence, all differences are mistakenly attributed to treatment effects (Wiens and Parker 1995). By specifying that certain variables will be measured while others will not, the results of a study may be constrained, enhancing the likelihood that one will find what one expects (or wants) to find. Whether or not values are implicit in the questions we ask, the study design and analysis must be rigorous and unbiased. Weak or biased study designs lead to weak or biased "scientific evidence," which is worse than worthless in environmental debates.

Perhaps the most pernicious and subtle effect of advocacy is on the interpretation of results. Even if a study is objectively framed and conscientiously designed and analyzed, the findings still must be placed in a context. Rousseau (1992) drew attention to what he called "pathological science," in which researchers unknowingly lose their objectivity in interpreting data that are near detection limits when much is riding on the results. Advocacy can reinforce this tendency, particularly because environmental debates are often emotionally charged. We care about the environment; that is why many of us became ecologists in the first place. Faced with the uncertainty that characterizes most findings in ecological research, it is all too easy for these feelings to influence how we view data, which results we choose to emphasize or to disregard, or whether what begins as speculation becomes transformed into "fact" because it is consistent with an advocacy position.

The responsibility of the ecologist, then, is to do science, and to do it as rigorously and objectively as possible. We must accept what our results tell us, not what our emotions might say. This is not to say that ecologists must retreat into the ivory tower and refrain from taking positions in environmental debates. There is an urgent need to bring scientific evidence to bear on environmental and management issues. These issues are so pressing that ecologists have a responsibility not to remain quiet when their findings can contribute to the debate. We should communicate the results of our science clearly and vigorously, in understandable terms, to the public and policy arenas. In so doing, however, there is also the paramount responsibility to recognize our own advocacy and to distinguish clearly between statements that are based on science and those that are based on personal values or viewpoints (Pitelka and Raynal 1989, Murphy and Noon 1991). We might take our lesson from the atomic scientists who, following the development of atomic energy at the end of the Second World War, spoke out frequently and vigorously about the potential abuses of this power, without compromising or distorting the science itself.

Ultimately, of course, ecological science is only one of many inputs to the development of management protocols or environmental policy. Some of these inputs reflect advocacy positions based on economics, religious beliefs, or political agendas. As ecologists, our agenda should be science, and our responsibility is to ensure that scientific findings carry the greatest possible weight in societal decisions about the environment.

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Young Scholar Dialogue

Ecology, Ethics, and Advocacy

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NOWHERE TO RUN, NOWHERE TO HIDE

Anthropogenic global change is radically altering climate, mineral cycles, land cover, and biotic communities (Turner et al. 1993, Vitousek 1994). These changes ensure that everywhere on Earth is affected by human actions. In some areas, such as the center of large cities, human transformation is near absolute, whereas in other places, such as remote parks, human influence is felt chiefly through the alteration of global cycles. However, no place is free from multiple, confounded human impacts. Consequently, ecological studies, whether they attend to or not, are partially studying the impact of anthropogenic change.

Ecologists cannot ignore these changes. First, ignoring these changes will produce flawed science; if ecologists ignore anthropogenic influences, they will probably attribute change to the wrong processes. Second, and perhaps more important, if ecologists want to guide or "engineer" the human transformation of the earth to reduce unintended consequences, they need to understand how ecosystems organize and function in response to a huge variety of anthropogenic alterations.

Engineering ecological systems is dangerous. Nature is neither predictable nor inert; rather it is evolutionary and self-modifying. History, evolution, and variation are all central to ecology, but foreign to the "memory-less," repeatable, and variation-minimizing methods of traditional engineering.

Ecologists cannot hide behind "pure" science and divorce themselves from the dangerous application of ecology. Whether ecologists like it or not, managers, policy makers, and the general public use ecological theory, or at least their understanding of ecological theory, to make decisions. To promote "reflective" management and sound science, ecologists need to study, criticize, and inform the human transformation of nature.

COMMUNICATING AN ECOLOGICAL WORLDVIEW

Improving the quality of ecological decision making requires that ecologists effectively communicate not only with land managers but also with a broad community of stakeholders involved in ecological transformation. Ecologists need to communicate and work with citizens, community associations, corporations, NGOs, politicians, government officials, and professional organizations. Ecologists should not enter naively into these interactions, but should be aware of the conflicting values and goals of different stakeholders (including scientists). Because of differences in these values and interests, any policy or management action is likely to produce winners and losers. Consequently, stakeholders will attempt to use science as a tool to manipulate the decision making process to their advantage. Ecologists, therefore, need to communicate ecological understanding clearly, or the unintended consequences of their actions may return to haunt them. Along with risks, politically charged decisions also offer opportunities for ecological intervention. Although some groups may value ignorance, most groups prefer to make informed decisions. By criticizing ecological ignorance and enriching ecological understanding, ecologists can often improve the quality, and potentially the equity, of decision making processes.

Ecologists need to communicate more than ecological "facts" or management prescriptions. They need to provide a basic understanding of ecology. It is particularly important to emphasize the differences between an ecological worldview that focuses on historical contingency, population uniqueness, and irreversibility and a mechanistic worldview that emphasizes repeatability, replaceablity, and reversibility (Mayr 1991). These differences are important, because they explain how ecological systems differ from physical systems and, therefore, how ecosystem transformations differ from mechanical transformations. Unless they provide this context, ecologists will not be able to convince managers to plan for surprises, to invest in learning, or to take a sophisticated approach to risk.

Models can provide particularly useful tools for synthesis and communication among different people. Models can be qualitative worldviews that propose one way the world may work, or models can be more testable amalgamations of assumptions and knowledge, such as mathematical formulae and computer simulations. As Walker mentions, models provide a means of "reflection" on the possible consequences and uncertainties associated with actions before they are undertaken in actuality.

The effective use of models requires a diversity of modeling approaches, the consideration of alternative models, and the continual testing and revision of models. Different types of models are appropriate for different types of communication. For example, a model that allows specialized scientists to test ecological hypotheses would probably not be useful at a public meeting for addressing the equity of a potential ecological impact . Alternative models are necessary; unless people have clearly articulated alternatives from which to choose, there is no opportunity for learning or change. Additionally, without alternatives, people may believe that they are using the "right" model, rather than one of a set of competing or provisional models. Models need to be continually revised, modified, and discarded based upon how they fare in tests against empirical data (Hilborn and Mangel 1997). Stated simply, models are useful if they are used within some sort of "adaptive management" framework that focuses on using a modeling process, rather than a specific model, to learn how a system works.

WRESTLING WITH REAL-WORLD QUESTIONS

Traditional engineering uses physical rules to manipulate the world and, consequently, it has benefited from advances in physics. Physicists have had great success in developing scaling rules that explain the behavior of physical systems over a wide range of scales. As we discussed, many people have a similarly mechanistic view of nature, leading them to hope that ecological scaling laws can be derived that would inform management the way physics informs engineering (Bak 1996). However, ecological research has demonstrated that different processes dominate at different spatial and temporal scales (Levin 1992). Although interesting in its own right, this scale variance makes it difficult to predict how processes will interact across scales, or how ecological understanding at one scale can be transformed to be applied at another scale.

scale can be transformed to be applied at another scale.

These scaling differences mean that ecological engineering has more diffuse and less tractable negative externalities (e.g., irrigation leading to the spread of river blindness) than does traditional engineering (e.g., a bridge collapsing due to an unexpected load). In traditional engineering systems, failure is often local, abrupt, and catastrophic, whereas "failure" in ecological systems often occurs gradually over larger areas. The chronic and diffuse nature of ecological degradation makes dealing intelligently and equitably with the unpredictable, the unknown, and surprising aspects of ecosystems difficult, but this does not obviate the need to actually make decisions and manage these systems.

Ecologists must use redundancy, diversity, and the production of novelty to hedge against surprise. Engineers traditionally have attempted to avoid disaster by "fail-safe" design (e.g., over-building a bridge by a safety factor), but we know that there is no "fail-safe" strategy for ecological management. Ecological management plans need to be "safe-fail," and this goal requires diverse, rather than efficient, management.

Ecological management needs to combine a diversity of approaches within an experimental setting. Diversity reduces the cost of any individual failure, and an "experimental" setting allows scientists to analyze the consequences of management. Experimental management requires replicated management treatments that can be compared against controls to test competing hypotheses (Walters and Holling 1990). In the short term, management that follows "best practices" is cheaper than experimental management techniques, but a monolithic approach reduces the ability of management to improve, leaving it vulnerable to change. The capacity of experimental management to adapt and learn provides it with a better chance of avoiding the disasters that often beset monolithic management. Over longer periods of time, the adaptability of experimental management makes it both cheaper and safer than monolithic management.

Ecologists can also learn from previous interventions in other systems. Although each situation is unique, there are also similarities among situations that can inform intervention. To utilize existing information effectively, ecologists must develop the statistical and modeling sophistication to integrate known, or prior, information into their analyses (Dixon and Ellison 1996).

A DIVERSITY OF APPROACHES

Baskerville advocates that scientists pay more attention to the scales of managers, while Wiens argues that managers should pay more attention to ecological scales. We propose that ecologists and managers should view management interventions as opportunities to learn how ecosystems function at different scales. Management interventions provide ecologists with opportunities to integrate small-scale understanding or experience with the larger scales that increasingly influence many resource management problems, but exceed the time frames and budgets of the average researcher. Such integration offers opportunities for theoretical advance, as well as for solutions to directly applied questions. We are not suggesting that applied ecology should be the only ecology practiced. Ecosystems are not defined by the bounds of a management plan. The scales of human impacts do not always coincide with the scales of key ecological processes, nor do management questions fully define ecological issues (e.g., studying the impacts of new logging strategies on the forest may not consider impacts to salmon populations). To advance, ecology must encourage a diversity of approaches.

Ecology needs to expand to include the large without abandoning the small. Ecological research must range from the natural history and behavior of a single species to regional experiments. Small-scale experiments and species-specific research remain crucial to our understanding of biological processes at management scales. As Walker noted, it would be dangerous to solely address management questions: "If all scientists do is work on today's problems with managers, we run the risk of not developing new ideas and understanding about ecosystem ecology." A diverse ecology requires a diversity of researchers. All questions cannot be efficiently addressed by the same set of skills. Ecology requires, therefore, a diversity of ecologists and ecological practitioners. Ecologists should fear limited "cultural diversity" in science and resource management, just as we fear a simplification of biodiversity in nature.

ADVOCACY AND SCIENCE

Ecologists are frequently confronted with situations that they feel are wrong. However, it is difficult to decide when advocacy is an appropriate role for a scientist. As informed individuals, ecologists abandon the duties of citizenship if we hide our values behind a veil of scientific objectivity. However, if ecologists use scientific standing to advance appealing, but scientifically unsound, arguments, we abandon professionalism and scientific ethics.

Science in the service of decision making requires different outputs than science done without such a goal (Walters 1986). Ecologists need to be especially aware of the possibilities of type I (accepting a false hypothesis) and type II error (rejecting a true hypothesis) when the consequences of these different types of error may be unequal. For example, if rejecting a true hypothesis would result in an action with a much higher cost than accepting a false hypothesis, it is sensible to design an experiment and analyses to take those considerations into account. Ultimately, ecologists should be driven by professional standards so that an ecologist would feel comfortable with her methods even if they were used by someone else to advance an opposing hypothesis (e.g., her work for Greenpeace should be held to the same standards that she would expect from ecologists working for Exxon). Our advocacy may direct us to particular questions, but it should not instruct our answers.

Ecologists are not the only ones who need to be held to higher standards. Often, in the face of deadlines or political pressures to act, management policy is developed by picking the politically expedient aspects of ecological theory (e.g., "disturbance is natural"). Ecologists need to hold managers, policy makers, and the public accountable to the full scope of an ecological theory, with all its alternative hypotheses, confidence intervals, and context specificity.

Managers cannot simply claim to be "practitioners" who carry out the plans recommended to them by the scientists and policy makers. Managers need to be both practitioners and scientists; they need to join ecologists in understanding how humanity is altering ecological systems. They need to learn to operate with alternative testable hypotheses and to work for change, rather than to build barriers against it.

BARRIERS AND BRIDGES

Scientists who want to improve the management of ecological systems need to better understand the decision making process and to combine ecological knowledge with concepts from non-ecological fields such as economics, finance, ethics, planning, and anthropology. An increased demand for cross-disciplinary and collaborative work to address complex, real-world problems carries with it an increased demand to be able to communicate and learn from people from other backgrounds and with other worldviews.

Ecologists need to become better at communication if non-ecologists and ecologists are going to work together to advance ecological theory and practice. Journal publication is an efficient way to communicate among scientists, but a poor route for communicating new findings in ecological science to policy makers, managers, or the public. Journal articles are difficult to obtain, understand, or apply. These barriers slow the spread of ecological knowledge from the active research community. Journals also afford no reasonable mechanism for dialogue with the policy and applied realms.

Collaboration and communication are risky for ecologists, because they take energy away from studying ecology. If too much emphasis is placed on understanding all fields and issues that impinge upon ecology, ecologists risk becoming jacks-of-all-trades who are masters-of-none. To maintain the integrity of ecology as a discipline, ecology needs to maintain a strong scientific focus and champion science that is repeatable and methodologically objective.

Applied research opportunities for young scientists should be increasing, with the ecological transformation of the Earth and the attendant problems that this transformation brings. However, reversing ecological degradation often is considered a luxury, in part due to the difficulty in creating reversing ecological degradation often is considered a luxury, in part due to the difficulty in creating effective market mechanisms to efficiently and equitably distribute the benefits and costs of ecological transformation.

REFLECT BEFORE ACTING, BUT ACT

Baskerville condemns ecological management as "inadequate reflection before action." This statement may become the epitaph of human civilization, but ecologists should not let future generations say that the world was destroyed by "a lack of action after a lot of reflection." If ecologists wish to alter the way in which the world is being transformed by human activities, then we must begin by identifying problems and offering to help work toward solutions.

Ecology is still a young science. Little is known about how ecosystems function, and even less about the consequences of anthropogenic global change. Applied ecology offers great opportunities to acquire ecological understanding, but non-applied ecology also offers many rewards. It is vital that ecologists be aware of their role in supplying the theoretical underpinnings for a more reasoned transformation of the Earth's ecological systems, even if they do not work directly on that transformation themselves. No one person can do it all, but ecologists working together, with other scientists, managers, companies, governments, and the public, have the potential to achieve a great deal.

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