The Golden Rule–a Proper Scale for Our Environmental Crisis

One among millions of species, we have a parochial, but legitimate, interest in our own survival

by Stephen Jay Gould

Patience enjoys a long pedigree of favor. Chaucer pronounced it "an heigh vertu, certeyn" ("The Franklin's Tale"), while the New Testament had already made a motto of the Old Testament's most famous embodiment: "Ye have heard of the patience of Job" (James 5:11). Yet some cases seem so extended in diligence and time that another factor beyond sheer endurance must lie behind the wait. When Alberich, having lost the Ring of the Nibelungen fully three operas ago, shows up in act 2 of *Götterdämmerung* to advise his son Hagen on strategies for recovery, we can hardly suppress a flicker of admiration for this otherwise unlovable character. (I happen to adore Wagner, but I do recognize that a wait through nearly all the *Ring* cycle would be, to certain unenlightened folks, the very definition of eternity in Hades.)

Patience of this magnitude usually involves a deep understanding of a fundamental principle, central to my own profession of geology but all too rarely grasped in daily life—the effects of scale. Phenomena unfold on their own appropriate scales of space and time and may be invisible in our myopic world of dimensions assessed by comparison with human height and times metered by human life spans. So much of accumulating importance at earthly scales—the results of geological erosion, evolutionary changes in lineages—is invisible by the measuring rod of a human life. So much that matters to particles in the microscopic world of molecules—the history of a dust grain subject to Brownian motion, the fate of shrunken people in *Fantastic Voyage* or *Inner Space*—either averages out to stability at our scale or simply stands below our limits of perception.

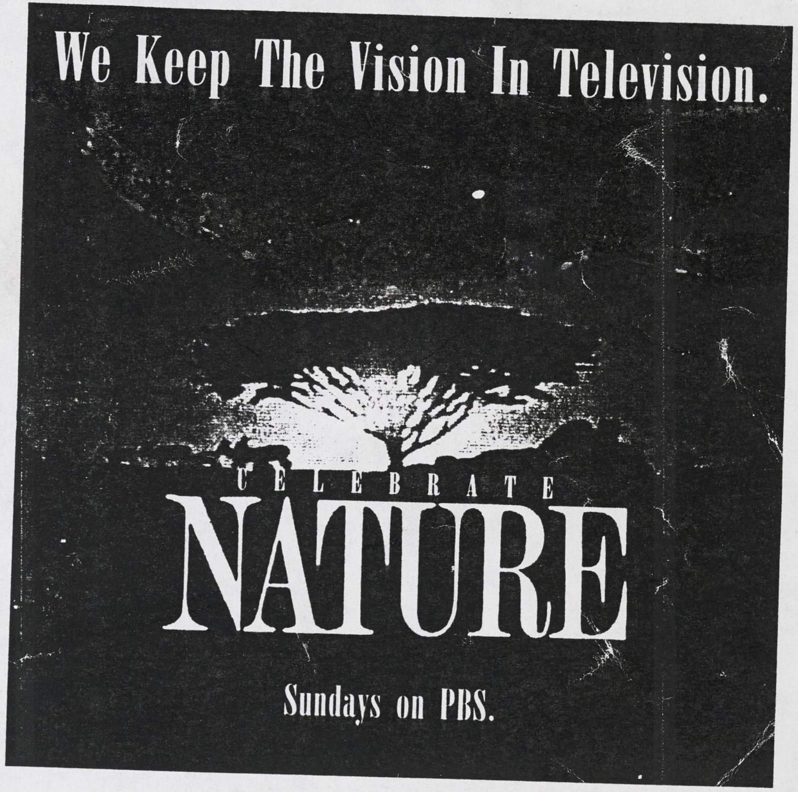
It takes a particular kind of genius or deep understanding to transcend this most pervasive of all conceptual biases and to capture a phenomenon by grasping a proper scale beyond the measuring rods of our own world. Alberich and Wotan know that pursuit of the Ring is dynastic or generational, not personal. William of Baskerville (in Umberto Eco's *Name of the Rose*) solves his medieval mystery because he alone understands that, in the perspective of centuries, the convulsive events of his own day (the dispute between papacies of Rome and Avignon) will be forgotten, while the only surviving copy of a book by Aristotle may influence millennia. Architects of medieval cathedrals had to frame satisfaction on scales beyond their own existence, for they could not live to witness the completion of their designs.

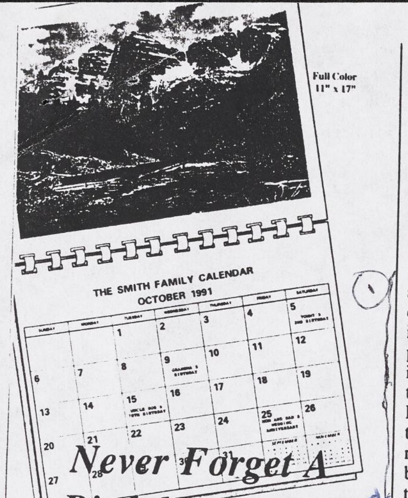
May I indulge in a personal anecdote on the subject of scale? As a child, I loved to memorize facts but rebelled at those I deemed unimportant (baseball stats were in, popes of Rome and kings of England out). In sixth grade, I had to memorize the sequence of land acquisitions that built America. I could see the rationale for learning about the Louisiana Purchase and the Mexican Cession—since they added big chunks to our totality. But I remember balking, and publicly challenging the long-suffering Ms. Stack, at the Gadsden Purchase of 1853. Why did I have to know about a sliver of southern Arizona and New Mexico?

Now I am finally hoist by my own petard (blown up by my own noxious charge, according to the etymologies). After a lifetime of complete nonimpact by the Gadsden Purchase, I have become unwittingly embroiled in a controversy about a tiny bit of territory within this smallest of American growing points. A little bit of a little bit; so much for effects of scale and the penalties of blithe ignorance.

The case is a classic representative of a genre (environmentalists versus developers) made familiar in recent struggles to save endangered populations—the snail darter of a few years back, the northern spotted owl versus timber interests (decided, properly in my view, for the birds on the day that I write this essay, June 23, 1990). The University of Arizona, with the backing of an international consortium of astronomers, wishes to build a complex of telescopes atop Mount Graham in southeastern Arizona (part of the Gadsden Purchase). But the old-growth spruce-fir habitat on the mountaintop forms the heart of the range for *Tamiasciurus hudsonicus grahamensis*, the Mount Graham red squirrel—a distinct subspecies that lives nowhere else and that forms the southernmost population of the entire species. The population has already been reduced to some 100 survivors, and destruction of several acres of spruce-fir growth (to build the telescopes) within the 700 or so remaining acres of best habitat might well administer a *coup de grâce* to this fragile population.

I cannot state an expert opinion on details of this controversy (I have already confessed my ignorance about everything involving the Gadsden Purchase and its legacy). Many questions need to be answered. Is the population already too small to survive in any case? If not, could





the population, with proper management, coexist with the telescopes in the remaining habitat? (Environmentalists fear change of microclimate as much or more than loss of acreage. Reduction of forest canopy will increase wind and sun, producing a drop in humidity. The squirrels survive winter by storing unopened cones in food caches beside trees. If humidity falls, cones may dry out and open, causing loss of seeds and destruction of food.)

① I do not think that, practically or morally, we can defend a policy of saving every distinct local population of organisms. I can cite a good rationale for the preservation of species—for each species is a unique and separate natural object that, once lost, can never be reconstituted. But subspecies are distinct local populations of species with broader geographical ranges. Subspecies are dynamic, interbreedable, and constantly changing; what then are we saving by declaring them all inviolate? Thus, I confess that I do not agree with all arguments advanced by defenders of the Mount Graham red squirrel. One leaflet, for example, argues: "The population has been recently shown to have a fixed, homozygous allele which is unique in Western North America." Sorry folks. I will stoutly defend species, but we cannot ask for the preservation of every distinctive gene, unless we find a way to abolish death itself (for many organisms carry unique mutations).

No, I think that for local populations of species with broader ranges, the brief for preservation must be made on a case by case basis, not a general principle of preservation (lest the environmental movement ultimately lose popular support for trying to freeze a dynamic evolutionary world *in statu quo*). On this proper basis of individual merit, I am entirely persuaded that the Mount Graham red squirrel should be protected and the astronomical observatory built elsewhere—and for two reasons.

② First, the squirrel itself: the Mount Graham red is an unusually interesting local population within an important species. It is isolated from all other populations and forms the southernmost extreme of the species' range. Such peripheral populations, living in marginal habitats, are of special interest to students of evolution.

Second, the habitat: environmentalists continually face the political reality that support and funding can be won for soft, cuddly, and "attractive" animals, but not for slimy, grubby, and ugly creatures (of potentially greater evolutionary interest and practical significance) or for habitats. This situation has led to the practical concept of "umbrella" or "indicator" species—surrogates for a larger ecological entity worthy of preservation. Thus, the giant panda (really quite a boring and ornery creature despite its good looks) raises money to save the remaining bamboo forests of China (and a plethora of other endangered creatures with no political clout); the northern spotted owl has just rescued some magnificent stands of old-growth giant cedars, Douglas fir, and redwoods (and I say hosanna); and the Mount Graham red squirrel may save a rare and precious habitat of extraordinary evolutionary interest.

The Pinaleno Mountains, reaching 10,720 feet at Mount Graham, are an isolated fault-block range separated from others by alluvial and desert valleys that dip to less than 3,000 feet in elevation. The high peaks of the Pinalenos contain an important and unusual fauna for two reasons. First, they harbor a junction of two biogeographic provinces: the Nearctic, or northern, by way of the Colorado Plateau, and the Neotropical, or southern, via the Mexican Plateau. The Mount Graham red squirrel (a northern species) can live this far south because high elevations reproduce the climate and habitat found near sea level in the more congenial north. Second, and more important to evolutionists, the old-growth spruce-fir habitats on the high peaks of the Pinalenos are isolated "sky islands"—10,000-year-old remnants of a habitat more widely spread over the region of the Gadsden Purchase during the height of the last Ice Age. In evolutionary terms, these isolated pieces of habitat are true islands—patches of more northern microclimate surrounded by southern desert. They are functionally equivalent to bits of land in the ocean. Consider the role that islands (like the Galápagos) have played both in developing the concepts of evolutionary theory and in acting as cradles of origin (through isolation) or vestiges of preservation for biological novelties.

Thus, whether or not the telescopes will drive the Mount Graham red squirrel to extinction (an unsettled question well outside my area of expertise), the sky islands of the Pinalenos are precious habitats that should not be compromised. Let the Mount Graham red squirrel, so worthy of preservation in its own right, also serve as an indicator species for the unique and fragile habitat that it occupies.

But why should I, a confirmed eastern urbanite who has already disclaimed all concern for the Gadsden Purchase, choose to involve myself in the case of the Mount Graham red squirrel? The answer, unsurprisingly, is that I have been enlisted—involuntarily, unawares, and on the wrong

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side to boot. I am simply fighting mad, and fighting back.

The June 7, 1990, *Wall Street Journal* ran a prodevelopment, antisquirrel opinion piece by Michael D. Copeland (identified as "executive director of the Political Economy Research Center in Bozeman, Montana") under the patently absurd title: "No Red Squirrels? Mother Nature May Be Better Off." (I can at least grasp, while still rejecting, the claim that nature would be no worse off if the squirrels died, but I am utterly befuddled at how anyone could argue that the squirrels inflict a positive harm upon the mother of us all!) In any case, Copeland misunderstood my writings in formulating a supposedly scientific argument for his position.

Now, scarcely a day goes by when I do not read a misrepresentation of my views (usually by creationists, racists, or football fans, in order of frequency). My response to nearly all misquotation is the effective retort of preference: utter silence. (Honorable intellectual disagreement should always be addressed; misquotation should be ignored, when possible and politically practical.) I make an exception in this case because Copeland cited me in the service of a classic false argument—indeed, the standard, almost canonical misuse of my profession of paleontology in debates about extinction. Paleontologists have been enlisted again and again, in opposition to our actual opinions and in support of attitudes that most of us regard as anathema, to uphold arguments by developers about the irrelevance (or even, in this case, the benevolence) of modern anthropogenic extinction. This standard error is a classic example of failure to understand the importance of scale—thus I return to the premise and structure of my introductory paragraphs (did you really think that I waffled on so long about scale only so that I could talk about the Gadsden Purchase?).

Paleontologists do discuss the inevitability of extinction for all species—in the long run and on the broad scale of geological time. We are fond of saying that 99 percent or more of all species that ever lived are now extinct. (My colleague Dave Raup often opens talks on extinction with a zinging one-liner: "To a first approximation, all species are extinct.") We do therefore identify extinction as the normal fate of species. We also talk a lot—more of late since new data have made the field so exciting—about the mass extinctions that punctuate the history of life from time to time. We do discuss the issue of eventual "recovery" from these extinctions, in the sense that life does rebuild or surpass its former diversity after several million years. Finally, we do allow that mass extinctions break up stable faunas and, in this sense, permit or even foster evolutionary innovations well down the road (including the dominance of mammals and the eventual origin of humans, following the death of dinosaurs).

From this set of statements about extinction in the fullness of geological time (on scales of millions of years), some apologists for development have argued that extinction at any scale (even of local populations within years or decades) poses no biological worry but, on the contrary, must be viewed as a comfortable part of an inevitable natural order. Or so Copeland states:

> Suppose we lost a species. How devastating would that be? "Mass extinctions have been recorded since the dawn of paleontology," writes Harvard paleontologist Stephen Gould . . . the most severe of these occurred approximately 250 million years ago . . . with an estimated 96 percent extinction of species, says Mr. Gould. . . . There is general agreement among scientists that today's species represent a small proportion of all those that have ever existed—probably less than 1 percent. This means that more than 99 percent of all species ever living have become extinct.

From these facts, largely irrelevant to red squirrels on Mount Graham, Copeland makes inferences about the benevolence of extinction in general (although the argument applies only to geological scales):

> Yet, in spite of these extinctions, both Mr. Gould and University of Chicago paleontologist Jack Sepkoski say that the actual number of living species has probably increased over time. [True, but not as a result of mass extinctions, despite Copeland's next sentence.] The "niches" created by extinctions provide an opportunity for a vigorous development of new species. . . . Thus, evolutionary history appears to have been characterized by millions of species extinctions and subsequent increases in species numbers. Indeed, by attempting to preserve species living on the brink of extinction, we may be wasting time, effort and money on animals that will disappear over time, regardless of our efforts.

But all will "disappear over time, regardless of our efforts"—millions of years from now for most species if we don't interfere. The mean life span of marine invertebrate species lies between 5 and 10 million years; terrestrial vertebrate species turn over more rapidly, but still average in the millions. By contrast, *Homo sapiens* may be only 250,000 years old or so and may enjoy a considerable future if we don't self-destruct. Similarly, recovery from mass extinction takes its natural measure in millions of years—as much as 10 million or more for fully rekindled diversity after major catastrophic events.

These are the natural time scales of evolution and geology on our planet. But what can such vastness possibly mean for our legitimately parochial interest in ourselves, our ethnic groups, our nations, our cultural traditions, our bloodlines? Of what conceivable significance to us is the prospect of recovery from mass extinction 10 million years down the road if our entire species, not to mention our personal family lineage, has so little prospect of surviving that long?

Capacity for recovery at geological scales has no bearing whatever upon the meaning of extinction today. We are not protecting Mount Graham red squirrels because we fear for global stability in a distant future not likely to include us. We are trying to preserve populations and environments because the comfort and decency of our present lives, and those of fellow species that share our planet, depend upon such stability. Mass extinctions may not threaten distant futures, but they are decidedly unpleasant for species in the throes of their power (particularly if triggered by such truly catastrophic events as extraterrestrial impact). At the appropriate scale of our lives, we are just a species in the midst of such a moment. And to say that we should let the squirrels go (at our immediate scale) because all species eventually die (at geological scales) makes about as much sense as arguing that we shouldn't treat an easily curable childhood infection because all humans are ultimately and inevitably mortal. I love geological time—a wondrous and expansive notion that sets the foundation of my chosen profession, but such immensity is not the proper scale of my personal life.

The same issue of scale underlies the main contributions that my profession of paleontology might make to our larger search for an environmental ethic. This decade, a prelude to the millennium, is widely and correctly viewed as a turning point that will lead either to environmental perdition or stabilization. We have fouled local nests before and driven regional faunas to extinction, but we have never been able to unleash planetary effects before our current concern with ozone holes and putative global warming. In this context, we are searching for proper themes and language to express our environmental worries.

I don't know that paleontology has a great deal to offer, but I would advance one geological insight to combat a well-meaning, but seriously flawed (and all too common), position and to focus attention on the right issue at the proper scale. Two linked arguments are often promoted as a basis for an environmental ethic:

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1. That we live on a fragile planet now subject to permanent derailment and disruption by human intervention;
2. That humans must learn to act as stewards for this threatened world.

Such views, however well intentioned, are rooted in the old sin of pride and exaggerated self-importance. We are one among millions of species, stewards of nothing. By what argument could we, arising just a geological microsecond ago, become responsible for the affairs of a world 4.5 billion years old, teeming with life that has been evolving and diversifying for at least three-quarters of that immense span? Nature does not exist for us, had no idea we were coming, and doesn't give a damn about us. Omar Khayyám was right in all but his crimped view of the earth as battered when he made his brilliant comparison of our world to an eastern hotel:

> Think, in this battered Caravanserai
> Whose Portals are alternate
> Night and Day,
> How Sultan after Sultan with his Pomp
> Abode his destined Hour, and
> went his way.

This assertion of ultimate impotence could be countered if we, despite our late arrival, now held power over the planet's future (argument number one above). But we don't, despite popular misperception of our might. We are virtually powerless over the earth at our planet's own geological time scale. All the megatonnage in our nuclear arsenals yield but one ten-thousandth the power of the asteroid that might have triggered the Cretaceous mass extinction. Yet the earth survived that larger shock and, in wiping out dinosaurs, paved the road for the evolution of large mammals, including humans. We fear global warming, yet even the most radical model yields an earth far cooler than many happy and prosperous times of a prehuman past. We can surely destroy ourselves, and take many other species with us, but we can barely dent bacterial diversity and will surely not remove many million species of insects and mites. On geological scales, our planet will take good care of itself and let time clear the impact of any human malfeasance. The earth need never seek a henchman to wreak Henry's vengeance upon Thomas à Becket: "Who will free me from this turbulent priest?" Our planet simply waits.

People who do not appreciate the fundamental principle of appropriate scales often misread such an argument as a claim that we may therefore cease to worry about environmental deterioration—just as Copeland argued falsely that we need not fret about extinction. But I raise the same counterargument. We cannot threaten at geological scales, but such vastness is entirely inappropriate. We have a legitimately parochial interest in our own lives, the happiness and prosperity of our children, the suffering of our fellows. The planet will recover from nuclear holocaust, but we will be killed and maimed by the billions, and our cultures will perish. The earth will prosper if polar icecaps melt under a global greenhouse, but most of our major cities, built at sea level as ports and harbors, will founder, and changing agricultural patterns will uproot our populations.

We must squarely face an unpleasant historical fact. The conservation movement was born, in large part, as an elitest attempt by wealthy social leaders to preserve wilderness as a domain for patrician leisure and contemplation (against the image, so to speak, of poor immigrants traipsing in hordes through the woods with their Sunday picnic baskets). We have never entirely shaken this legacy of environmentalism as something opposed to immediate human needs, particularly of the impoverished and unfortunate. But the Third World expands and contains most of the pristine habitat that we yearn to preserve. Environmental movements cannot prevail until they convince people that clean air and water, solar power, recycling, and reforestation are best solutions (as they are) for human needs at human scales—and not for impossibly distant planetary futures.

I have a decidedly unradical suggestion to make about an appropriate environmental ethic—one rooted, with this entire essay, in the issue of appropriate human scale versus the majesty, but irrelevance, of geological time. I have never been much attracted to the Kantian categorical imperative in searching for an ethic—to moral laws that are absolute and unconditional and do not involve any ulterior motive or end. The world is too complex and sloppy for such uncompromising attitudes (and God help us if we embrace the wrong principle, and then fight wars, kill, and maim in our absolute certainty). I prefer the messier "hypothetical imperatives" that invoke desire, negotiation, and reciprocity. Of these "lesser," but altogether wiser and deeper, principles, one has stood out for its independent derivation, with different words but to the same effect, in culture after culture. I imagine that our various societies grope toward this principle because structural stability, and basic decency necessary for any tolerable life, demand such a maxim. Christians call this principle the "golden rule"; Plato, Hillel, and Confucius knew the same maxim by other names. I cannot think of a better principle based on enlightened self-interest. If we all treated others as we wish to be treated ourselves, then decency and stability would have to prevail.

I suggest that we execute such a pact with our planet. She holds all the cards and has immense power over us—so such a compact, which we desperately need but she does not at her own time scale, would be a blessing for us, and an indulgence for her. We had better sign the papers while she is still willing to make a deal. If we treat her nicely, she will keep us going for a while. If we scratch her, she will bleed, kick us out, bandage up, and go about her business at her planetary scale. Poor Richard told us that "necessity never made a good bargain," but the earth is kinder than human agents in the "art of the deal." She will uphold her end; we must now go and do likewise.

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J. Med. Microbiol. — Vol. 32 (1990), 239–242

0022–2615/90/0032–0239/$10.00

A probable waterborne outbreak of cryptosporidiosis in the Sheffield area

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Summary. There was a marked peak in human cases of cryptosporidiosis in the Sheffield area in May and June 1986. Extensive epidemiological investigations failed to find a common source of food or a consistent history of animal contact, but did suggest that a waterborne outbreak of cryptosporidiosis may have occurred. Cryptosporidium oocysts were found in untreated water and in fish from a reservoir complex implicated by epidemiological analysis. Laboratory investigations confirmed that cattle on a farm adjacent to the reservoir complex were a possible source of contamination.

Introduction

The coccidian parasite, *Cryptosporidium*, is now recognised as an important intestinal pathogen causing acute diarrhoeal disease in man.[1] The source of infection for man may be diverse. Infections in farm, domestic and laboratory animals are common,[2–4] and early reports suggested that close contact with animals was the usual source of infection for man.[5,6] Transmission of *Cryptosporidium* from animals to man *via* food and milk has been documented[7,8] and person-to-person transmission of *Cryptosporidium* has been reported in hospitals and nurseries.[9,10] Of major public health concern are reports,[11,12] supported by epidemiological and environmental evidence, of possible transmission of *Cryptosporidium via* contaminated drinking water treated by conventional means to remove bacterial and viral pathogens.

In the Sheffield area, from late April to October 1986, we observed an increase in human cases of cryptosporidiosis, with a marked peak in May and June. No changes in laboratory methods for detecting cryptosporidium oocysts took place at that time. Extensive epidemiological investigations by Sheffield Environmental Health Department (EHD) failed to find a common source of food or milk, or a consistent history of close contact with animals. However, of 62 patients recognised in May or June, 49 (79%) drank water from the same reservoir complex.

The purpose of this study was to determine whether the hypothesis of a waterborne outbreak of cryptosporidiosis in Sheffield could be supported.

Materials and methods

Selection of samples

Man. All faecal samples from human cases of acute diarrhoea submitted to Sheffield Public Health Laboratory (PHL) between January 1985 and December 1987 were examined for oocysts of *Cryptosporidium* and for other recognised intestinal pathogens.

Cattle. Faecal samples from cattle on a farm adjacent to the implicated reservoir complex were taken by the Veterinary Investigations Centre (VIC), Loughborough, where smears were stained by a modified Ziehl-Neelsen (ZN) method, and examined microscopically.

Fish. Wild brown trout (*Salmo trutta*) were netted from the reservoir complex by the Yorkshire Water Authority (YWA). Intestinal contents were removed into sterile universal containers and examined at Sheffield PHL.

Water. Pre- and post-treatment samples of water (10 or 20 L depending on turbidity) were collected by YWA from the two reservoirs in the complex, feeder streams flowing into the reservoirs, a river flowing out of the reservoirs, and children's paddling pools fed by the latter river. Water samples were examined at Sheffield PHL.

Examination of faecal samples

All human faecal and fish intestinal samples were examined for oocysts of *Cryptosporidium* by microscopic examination of a direct smear stained by a modified ZN method.[13] Samples containing bodies resembling such oocysts were tested by a direct immunofluorescence (IF) method, with mouse IgM monoclonal antibody (MAb)

Received 6 Nov. 1989; accepted 15 Jan. 1990.

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Transactions of the American Fisheries Society 120:816–827, 1991

Reproductive Success of Hatchery and Wild Steelhead

Chilcote et al. (1986) used an allozyme locus to study the survival and reproductive success of hatchery steelhead *Oncorhynchus mykiss* under natural conditions. They concluded (1) that observed genotypic deviations from expected Mendelian ratios for progeny of hatchery steelhead were due to differential survival of allozyme genotypes in the natural environment and (2) that the reproductive success of hatchery steelhead was substantially less than that of wild steelhead under natural conditions. We detected several methodological problems with their paper that made us question the validity of those two conclusions. In this comment, we present evidence that the deviations from Mendelian proportions most likely resulted from misidentification of subyearling coastal cutthroat trout *Oncorhynchus clarki clarki* as steelhead. This problem and others require a reestimation of the relative genetic contributions of hatchery and wild steelhead to wild progeny in the Kalama River, Washington. We use revised equations to reanalyze the data of Chilcote et al. (1986) and obtain results that uphold their second conclusion that hatchery steelhead had substantially lower reproductive success than wild steelhead.

Background

Considerable attention has been focused in recent years on the potential adverse effects of introduced hatchery fish on wild populations of salmonids (Reisenbichler and McIntyre 1977; Krueger et al. 1981; Leider et al. 1984, 1986, 1990; Campton and Johnston 1985; Chilcote et al. 1986; Levings et al. 1986). Concerns arise from the possibility that hatchery fish are less fit in natural environments than the wild conspecifics with which they may interbreed (Allendorf and Phelps 1980; Ryman and Stahl 1980; Cross and King 1983; Doyle 1983; Vuorinen 1984; Allendorf and Ryman 1987; Woodward and Strange 1987; Verspoor 1988). These concerns are particularly important in the Pacific Northwest, where millions of hatchery-produced smolts are released annually to enhance fisheries and natural populations of anadromous salmonids. However, few quantitative estimates of relative fitness are available for hatchery and wild fish in natural environments.

Chilcote et al. (1986) made one such estimate of relative fitness by comparing the genetic contributions to wild progeny made by naturally spawning hatchery and wild steelhead. Chilcote et al. released hatchery fish that were homozygous or heterozygous for an electrophoretically detectable allozyme occurring at low frequency (<0.11) in wild populations. They concluded (1) that "the success of hatchery fish in producing smolt offspring was only 28% of that for wild fish" and (2) that hatchery fish with the genetic mark were only 33–78% as fit in the wild as siblings homozygous for the common allele. The lower fitness was attributed to natural selection at the marker locus or at loci closely linked to the marker.

The results of Chilcote et al. (1986) have at least two important implications. First, they are central to the ongoing controversy regarding the relative fitness of hatchery and wild salmonids and thus could greatly affect the management of these fishes in the Pacific Northwest. Second, fishery biologists are citing those results as evidence of intense natural selection at allozyme loci (e.g., Chandler and Bjornn 1989). Some biologists are further arguing against the use of allozyme markers in genetic monitoring programs for hatchery fish (see reviews by Seeb et al. 1990 and Utter and Seeb 1990 regarding the merits of such programs). The findings of Chilcote et al. thus warrant close examination.

Effect of the Genetic Mark

As part of their study to assess the relative reproductive success of hatchery and wild steelhead, Chilcote et al. conducted a field experiment to test for survival differences among the three allozyme genotypes at the marker locus *G3PDH-1**, which codes the enzyme glycerol-3-phosphate dehydrogenase (enzyme number 1.1.1.8: IUBNC 1984; Chilcote et al. called this enzyme alpha-glycerol-phosphate dehydrogenase, coded by locus *AGP-1*). They crossed 13 males and 13 females that were heterozygous for the **100* and **140* alleles (their *A* and *A′* alleles) and released the progeny into four tributary creeks of the Kalama River. The creek sections stocked had no resident rainbow trout *Oncorhynchus mykiss*, and barrier falls

[1992]

POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	39	3–4*	279–287	1992

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DIET OVERLAP IN LARVAL LAKE HERRING (*COREGONUS ARTEDI*) AND BLOATERS (*COREGONUS HOYI*)

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ABSTRACT

The food preferences of larval lake herring (*Coregonus artedi*) and bloaters (*C. hoyi*) were compared in experiments in a small mesotrophic lake in southeastern Michigan. Diets of the two were increasingly similar as the experiment progressed until, by the end of 6.5 weeks, they were identical; Schoener's Index of diet overlap averaged 0.35 in the first week and reached 0.96 by the end of the study. In the first few weeks, lake herring ate mostly small cladocerans (*Bosmina longirostris*) and bloaters ate mostly cyclopoid copepodites. By the third week, both species ate small cladocerans (mostly *Chydorus sphaericus* and *Acroperus harpae*). At the conclusion of the study both species ate mostly large cladocerans (*Eurycercus lamellatus*). Strauss's selection index confirmed that lake herring actively fed on small cladocerans throughout the study and that bloaters relied more on cyclopoid copepods during the early part of the study and shifted to eating small and large cladocerans by the end. Both species had similar growth rates throughout the study and amount of consumed food was identical. The diet similarities of lake herring and bloater larvae could make them competitors for food in the Great Lakes, relieved only by a dissimilarity in hatching times and locations.

Key words: Great Lakes, *Coregonus*, competition, zooplankton, diet

1. INTRODUCTION

Eight species of whitefishes (*Coregonus*) were found in the Great Lakes as recently as the early 1950's (Todd 1986). Nearly all were important commercial species and important forage for the lake trout, *Salvelinus namaycush*. Since the 1950's, most species of *Coregonus* have completely disappeared in the Great Lakes (Todd 1986). Of the remaining species, lake whitefish (*C. clupeaformis*) and bloater (*C. hoyi*) are now very abundant, and lake herring (*C. artedi*) are only locally abundant (Fleischer 1992). Several factors have been implicated in the decline and extinction of *Coregonus* in the Great Lakes including: overfishing; predation from alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*), and sea lamprey (*Petromyzon marinus*); and competition from alewife, rainbow smelt, and other species of *Coregonus* (Anderson, Smith 1971; Smith 1972; Wells, McClain 1972). Until the late 1970's, similar causes may have been responsible for the low abundance of most species of *Coregonus*, but the resurgence of bloater and lake whitefish populations in the 1980's coupled with the continued decline of lake herring

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* Biology and Management of Coregonid Fishes, Thomas N. Todd and Miroslaw Luczynski [editors].

populations in Lakes Michigan and Huron suggested that these species had different limiting factors.

Bloater and lake herring are morphologically similar and have long been considered closely related (Koelz 1929). Introgressive hybridization between these two species is suspected in Lakes Michigan and Huron, further suggesting their close relationship (Todd, Stedman 1989). At the present time, bloater far outnumber lake herring, and their close taxonomic relationship suggests that the abundant bloater could affect the much rarer lake herring by competition for limited food resources. Anderson and Smith (1971) indicated that competition for zooplankton between the larvae of lake herring, rainbow smelt, and bloater had a strong negative influence on the abundance of lake herring, and Hatch and Underhill (1988) suggested that larval mortality may be one reason for the continued low recruitment of adult lake herring.

The purpose of this study was to determine the degree of competition for food of larval lake herring and bloater by 1) comparing their preference for particular prey species, sizes, and quantities of zooplankton; and 2) determining the extent of diet overlap between the two species.

2. METHODS

Eggs were stripped from ripe adults of lake herring and bloater and mechanically fertilized with techniques from Leach (1924). Adult fecund lake herring were taken from gillnets in Lake Superior near Bayfield, Wisconsin, in December 1987 and adult fecund bloater were taken in trawl tows in Lake Michigan near Waukegan, Illinois, in January 1988. Fertilized eggs were placed in McDonald jars for incubation at mean temperatures of 2.4°C (SE 0.1) for lake herring and 7.6°C (SE 0.1) for bloaters. The eggs from the two species were incubated at different temperatures to synchronize hatching times (Berlin et al. 1977).

On April 18 and April 20, 1988, newly hatched lake herring and bloater were distributed among four 2 m^3 circular cages (1500 per cage), 1.5 m in diameter, 1 m high and made of 0.8 mm mesh netting. Lake herring were about 10.8 mm and bloater were about 10.0 mm at time of release in the cages. The cage experiments were conducted in Pickerel Lake, Washtenaw County, Michigan, a small mesotrophic lake that supports a population of native lake herring. Cages with fish larvae were tied immediately adjacent to cages without fish (controls). We used the control cages to monitor the difference between potentially available prey species inside and outside the cages.

Zooplankton and fish larvae were sampled at dusk two days a week. A 3.2 L Van Dorn bottle was used to sample zooplankton. Two replicates were taken in each cage and in the open lake during each visit. Samples were sieved through a 0.065 mm mesh bucket, rinsed into 0.5 L glass jars, and preserved in 10% formalin. During each visit twenty fish were taken from each cage with a dipnet, placed over ice in 1 L glass jars filled with lake water, and returned to the laboratory. Fish larvae were then transferred to Whirl-pak* plastic bags and stored at –70°C. Surface water temperature was routinely taken with a mercury thermometer and routine maintenance of the cages included a thorough scrubbing of the sides of the netting with a long-handled nylon brush on the day after sampling.

In the laboratory, zooplankton were identified and measured to the nearest 0.1 mm. Five fish per species were chosen at random from the twenty sampled on each date. Fish were weighed wet to the nearest 0.1 mg and measured to the nearest 0.1 mm. Stomach contents were excised and all prey were identified, counted, and measured to the nearest 0.1 mm when possible. Prey items were identified with techniques of Edmondson (1959) and Pennak (1978). Prey species were combined into higher taxonomic groups for computing selection indices. Linear food selection indices (Strauss 1979) for these groups as food categories were computed for both lake herring and

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* Mention of trade names does not imply Government endorsement of commercial products.

bloater for each visit. Strauss's Index – ($r_i - p_i$), where r_i – proportion of food category i in the diet, and p_i – proportion of food category i in the environment. Schoener's index (α) of diet overlap (Schoener 1970) was also computed for each visit as:

$$\alpha = 1 - 0.5\left(\sum_{i=1}^{n} |P_{xi} - P_{yi}|\right)$$

where P_{xi} – proportion of food category i in the diet of species x, P_{yi} – proportion of food category i in the diet of species y, and n – number of food categories. We used analysis of variance to compare the differences between the fish by amount and size of eaten prey, and the differences between the cages and the open lake by zooplankton·density and size.

3. RESULTS

Although the study was scheduled to last eight weeks, we terminated it after 6.5 weeks because of the death of over 90% of the fish. The mean surface temperature increased greatly in the first two weeks but leveled off in the last two weeks with a high of 23.6°C in the sixth week (Tab. I). An afternoon temperature of 27°C was recorded on a non-sampling day. Large mats of algae also grew inside each cage.

Table I. Mean length (± SD) and mean weight (± SD) of fish, mean number of prey in stomachs per fish (number of fish), and mean surface temperature of Pickerel Lake in April–June 1988

Week	Mean length (mm)		Mean weight (mg)		Mean number of prey eaten		Surface temp. t (°C)
	Herring	Bloater	Herring	Bloater	Herring	Bloater	
1	11.3 (1.0)	10.3 (.4)	10.7 (3.3)	6.2 (2.0)	3.2 (15)	1.9 (10)	9.5
2	13.1 (1.4)	13.0 (1.1)	14.4 (4.7)	12.5 (4.0)	7.6 (15)	21.3 (10)	16.1
3	13.5 (1.4)	15.2 (1.6)	20.3 (7.0)	21.3 (6.9)	42.5 (15)	55.0 (10)	16.4
4	18.1 (3.1)	17.2 (1.9)	36.9 (23.7)	30.4 (11.0)	84.6 (5)	87.0 (5)	18.8
5	19.1 (2.1)	21.4 (2.6)	45.0 (18.7)	62.8 (32.1)	112.4 (20)	178.8 (14)	21.7
6	21.4 (2.6)	21.8 (2.5)	79.4 (29.9)	87.9 (40.6)	100.7 (10)	193.2 (5)	23.6
7	22.1 (3.3)	22.4 (6.3)	93.4 (52.6)	92.5 (88.9)	132.8 (5)	158.8 (9)	23.2

Zooplankton decreased significantly in the lake and in all cages throughout the study ($F_{(6,1584)} = 4.87$, $P < 0.01$). Zooplankton abundance was similar everywhere except for week 2 when zooplankton in the lake increased and zooplankton in the lake herring, bloater, and control cages decreased ($F_{(3,231)} = 43.13$, $P < 0.01$). Forty-seven invertebrate taxa excluding Rotifera were collected and combined into larger taxonomic groups: cyclopoid copepods (e.g., *Eucyclops agilis, Diacyclops thomasi, Tropocyclops prasinus*), calanoid copepods (e.g., *Skistodiaptomus oregonensis, Epischura lacustris*), copepod nauplii, small cladocerans (e.g., *Bosmina longirostris, Chydorus sphaericus, Acroperus harpae*), large cladocerans (e.g., *Eurycercus* *lamellatus, Ophryoxus gracilis*), daphniids (e.g., *Daphnia galeata mendotae, Simocephalus* spp.), and miscellaneous invertebrates. Both Rotifera and miscellaneous invertebrates were excluded from the analyses because they were less than 1% of the fish diets. Zooplankton density among the cages showed similar trends during the study. However, the zooplankton density in the lake differed at times (Fig. 1). While calanoid copepods in the cages decreased from the first to the seventh week, those in the lake remained high. Cyclopoid copepods showed a gradual decrease in density everywhere. Density of small cladocerans also decreased everywhere but was lowest in the lake ($F_{(3,341)}$ = 6.05, P <0.05). Density of large cladocerans was low everywhere until in the last two weeks, density increased in the lake and in the control cages. Daphniid densities were high in the first 3 weeks especially in the lake ($F_{(3,142)}$ = 78.37, P <0.01), but thereafter decreased. Copepod nauplii showed a gradual increase throughout the study everywhere.

Lake herring and bloater larvae grew at similar rates throughout the study (Tab. I). The length-weight regression equations were $W = 73.72 + 0.68L$ for herring, and $W = -99.68 + 8.30L$ for bloater. Herring grew at a faster rate in the first three weeks and bloater in the last four weeks; however, length and weights were equal at the end. The amount of food eaten by each fish was similar in pattern to the weight increase.

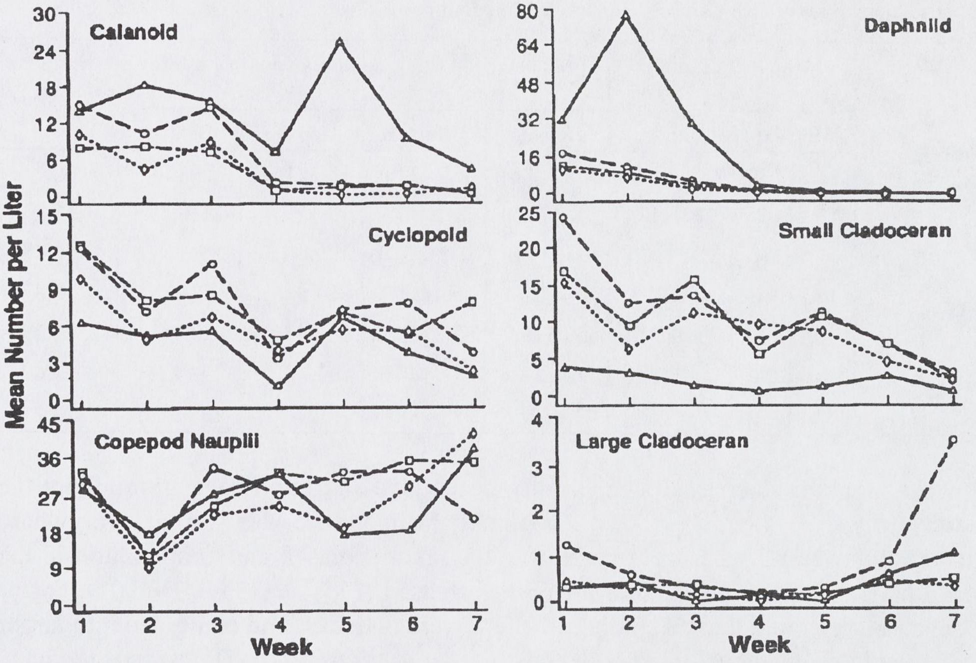

Fig. 1. Density of major zooplankton groups in Pickerel Lake and study cages in April–June 1988. Symbols refer to cage type as follows: triangle – open lake; circle – control; diamond – lake herring; are – bloater

Table II. Linear food selection indices for invertebrate groups in stomachs of lake herring and bloater in Pickerel Lake in April–June 1988, and diet overlap index between the fish species

Week	Fish	Calanoid	Cyclopoid	Daphniid	Lg. Clad[a]	Nauplii	Sm. Clad.	Overlap Index
1	Bloater	–0.085	0.268	0.370	–0.005	–0.404	–0.132	0.35
	Herring	–0.075	0.295	–0.005	0.014	–0.210	–0.019	
2	Bloater	–0.197	0.507	–0.131	–0.007	–0.210	0.038	0.48
	Herring	–0.105	0.055	–0.110	0.001	–0.210	0.401	
3	Bloater	–0.130	0.532	–0.050	0.008	–0.453	0.092	0.73
	Herring	–0.164	0.376	–0.032	0.002	–0.455	0.274	
4	Bloater	–0.029	0.016	0.041	0.007	–0.712	0.677	0.34[a]
	Herring	–0.022	0.016	–0.004	0.000	0.095	–0.053	
5	Bloater	–0.032	0.043	0.003	0.037	–0.619	0.566	0.93
	Herring	–0.005	–0.016	0.009	0.023	–0.571	0.560	
6	Bloater	–0.024	0.040	0.003	0.066	–0.773	0.687	0.91
	Herring	0.031	–0.002	0.014	0.053	–0.645	0.549	
7	Bloater	–0.000	0.082	0.002	0.549	–0.807	0.174	0.96
	Herring	–0.042	0.132	0.013	0.569	–0.880	0.208	

[a] Index calculated from two separate dates.

The most abundant prey in the fish stomachs were small cladocerans, cyclopoid copepods and large cladocerans. Lake herring ate mostly *B. longirostris* and varying proportions of cyclopoid copepodites, and *D. galeata mendotae* in the first 2.5 weeks, whereas bloaters mostly ate cyclopoid copepodites and varying proportions of *B. longirostris* and *T. prasinus*. In the third week the diet of both species abruptly switched to mostly *C. sphaericus; A. harpae*, cyclopoid copepodites and adult copepods were also eaten frequently. This pattern continued until the last week when *E. lamellatus* became dominant in stomachs of both fish species, though various copepods and small and large cladocerans were also eaten. Within the first three weeks, twelve lake herring and five bloaters had empty stomachs.

Bloaters consumed larger prey than lake herring in the first five weeks of the study, thereafter lake herring ate larger prey (Fig. 2); the overall difference was not significant ($F_{(1,11243)} = 4.80$, $P<0.12$). However, the interaction was significant ($F_{(6,11243)} = 36.38$, $P< 0.01$). The size of zooplankton in the lake was not significantly ($P>0.25$) different from the cages. Bloater and lake herring mean prey size was always larger than mean size of available prey inside the cages.

Although some differences were noted, food selection values and overall trends for both species were very similar throughout the study (Table II). Selection for

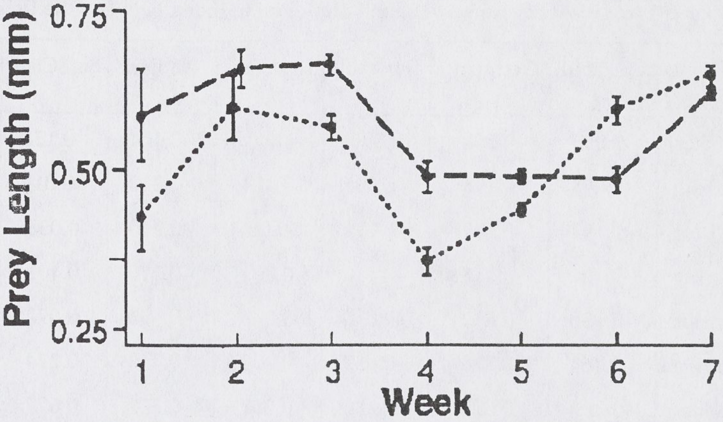

Fig. 2. Mean length and standard error of zooplankton prey in the stomachs of lake herring and bloater larvae in Pickerel Lake in April–June 1988. Means and error bars associated with the dotted line refer to lake herring and with the dashed line to bloater

cyclopoid copepods and copepod nauplii decreased throughout the study, whereas selection for small cladocerans increased. Calanoid copepods, daphniids, and large cladocerans were largely random selections except for large cladocerans in week 7.

The index of diet overlap strongly increased with time of the study (Table II). The first week index averaged 35%, but by the seventh week the index showed 96% overlap. We could not calculate index values for four of the thirteen sampling dates because we lacked samples for one or the other fish species. The fourth week index value was calculated from two different dates. Overlap was much less in the beginning of the study when zooplankton were more abundant than at the end.

4. DISCUSSION

Prey selection is defined as any difference between the environmental and dietary size and species distribution of prey (Eggers 1977). Bloater and lake herring ate the largest of the prey available in the cages throughout the study, and larger prey were increasingly preferred in the last several weeks, especially large cladocerans. Although the high positive selection of large cladocerans was partly a reflection of low density, they were numerically dominant in the fish stomachs in the seventh week. Daphniids were not preferred even when their abundance dropped. *Daphnia* spp. are more quickly digested than other crustaceans (Gannon 1976) and may have been missed as a result. The increased selection of small cladocerans was probably a result of their decreased density. The slight decrease in selection of cyclopoid copepods can be partly attributed to a lesser density decrease, however, this lesser decrease may be the result of both fish eating more small cladocerans than cyclopoid copepods. Non-selection of calanoid copepods may be attributable to size and speed; they are a large and very elusive prey (O'Brien 1979) and fish at this stage of life would find them hard to catch. Both species ate the most abundant of the largest prey that they could most easily capture. Confer and O'Bryan (1989) note that fish more likely feed on the largest prey that they can swallow.

Zooplankton in the lake were larger than zooplankton in the cages through most of the study. Daphniids were the main organisms in the lake and not present in the cages in the first four weeks, and calanoid copepods were the organisms in the last three weeks of the study. Cyclopoid copepods, copepod nauplii, and small cladocerans seemed to have free passage through the cage mesh because their densities were similar both inside and outside the cages. Some method of brushing the insides of the cages without harming the fish might have allowed for freer passage of the larger zooplankton.

Cage selectivity was a probable contributor to the demise of both lake herring and bloater in this study, although the long period of high temperatures (22°C) was a great factor and ultimately terminated the study one week early; the upper lethal temperature for lake herring is about 26°C (Edsall, Colby 1970). Zooplankton in the lake were almost twice as large as those in the cages except for weeks 4, 6, and 7. The lengths of all zooplankton decreased after the second week. As the fishes grew larger, their prey got smaller and less abundant. The large zooplankton, in particular, became less available to them at a size when they needed larger prey; unavailable zooplankton sizes at required times can result in heavy larval mortality (Taylor, Freeberg 1984). Warren and Lehman (1988) found YOY bloater switching to *Daphnia* after 20 mm. Inside the cages, lake herring and bloater, as they increased in size, decimated the numbers of the larger zooplankton probably to a level where it began affecting the fishes' growth and survival. Bloater and lake herring are resistant to starvation-induced mortality but their growth may be affected (Rice et al. 1987); the slower rate of growth in the fishes in the last few weeks may be an indication of insufficient food for growth. Growth even may have been retarded in earlier weeks because both herring and bloater did not average 16 mm total length until the fourth week, contrary to Pritchard (1930) who estimated most 16 mm lake herring average three weeks.

Although the indices measure different relationships, the increase in similarity of selection patterns in this study is shown by the large increase in the overlap index through time. Martin (1984) views 0.60 as the significant level for overlap. This increase in overlap may indicate a potential for competition for food between these species as juveniles – or may indicate a constriction of the available resource. However, an artificial situation was probably set up by these fishes being in cages; the small cladocerans in particular probably had enhanced production from the abundant algal growth inside the cages. Overlap is usually highest among competing species when food is most abundant and becomes least when food is in short supply (Schoener 1982), opposite to what happened in this study. The size selectivity of the cages probably restricted the bloater and lake herring juveniles from fully exercising their options for food as they would in the Great Lakes.

The possibility of competition for food between bloater and lake herring in the Great Lakes is lessened by differences in their spawning and hatching times and locations. Lake herring spawn in November–December in shallow waters and hatch after spring breakup of surface ice in March (Scott, Crossman 1973). In contrast, bloaters spawn in January–March and hatch in April–August and live below 73 m (Scott, Crossman 1973). Anderson and Smith (1971) found a negative effect on lake herring from competition with bloaters in western Lake Superior, but in most of the Great Lakes, the bulk of the herring hatch much earlier than bloaters. The earlier hatch should relieve both species from competing with each other. Although larval and juvenile lake herring and bloater are of a similar size and can eat the same type of food, the potential for competition between them is minimal. Competition for food with bloaters probably does not strongly contribute to low abundance of Great Lakes lake herring.

ACKNOWLEDGEMENTS

We thank M. Blouin for aid in obtaining and setting up the laboratory and field equipment, J. Miller for processing zooplankton samples, G. Fleischer for help in obtaining eggs and in the production of figures, A. Frank and J. Savino for statistical analyses, G. W. Eck, National Fisheries Research Center - Great Lakes, and M. G. Henry, University of Minnesota, for obtaining bloater eggs for us, and J. LaBossiere and Michigan Department of Natural Resources for permitting us to conduct our experiments in Pickerel Lake. Contribution 808 of the National Fisheries Research Center – Great Lakes.

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COMMENTARY

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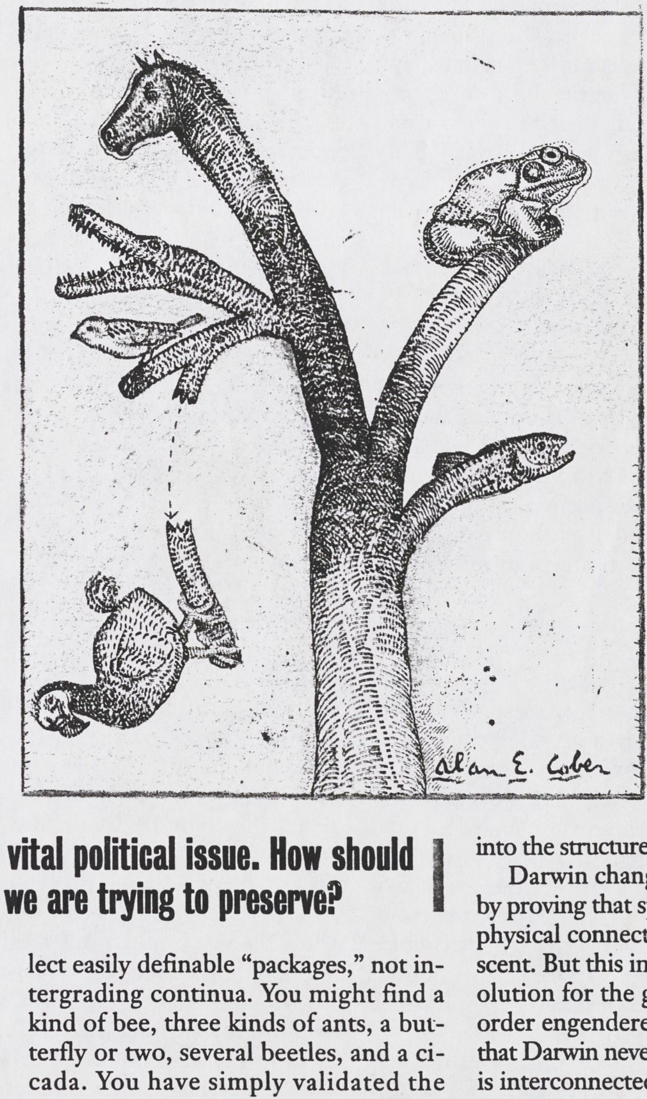
What Is a Species?

BY STEPHEN JAY GOULD

I HAD VISITED EVERY STATE BUT IDAHO. A FEW MONTHS AGO, I finally got my opportunity to complete the roster of 50 by driving east from Spokane, Washington, into western Idaho. As I crossed the state line, I made the same feeble attempt at humor that so many of us try in similar situations: "Gee, it doesn't look a bit different from easternmost Washington." ▪ We make such comments because we feel the discomfort of discord between our mental needs and the world's reality. Much of nature (including terrestrial real estate) is continuous, but both our mental and political structures require divisions and categories. We need to break large and continuous items into manageable units.



Many people feel the same way about species as I do about Idaho—but this feeling is wrong. Many people suppose that species must be arbitrary divisions of an evolutionary continuum in the same way that state boundaries are conventional divisions of unbroken land. Moreover, this is not merely an abstract issue of scientific theory but a pressing concern of political reality. The Endangered Species Act, for example, sets policy (with substantial teeth) for the preservation of species. But if species are only arbitrary divisions in nature's continuity, then what are we trying to preserve and how shall we define it? I write this article to argue that such a reading of evolutionary theory is wrong and that species are almost always objective entities in nature.

It's becoming a vital political issue. How should we define what we are trying to preserve?

Let us start with something uncontroversial: the bugs in your backyard. If you go out to make a complete collection of all the kinds of insects living in this small discrete space, you will collect easily definable "packages," not intergrading continua. You might find a kind of bee, three kinds of ants, a butterfly or two, several beetles, and a cicada. You have simply validated the commonsense notion known to all: in any small space during any given moment, the animals we see belong to separate and definable groups—and we call these groups species.

In the eighteenth century this commonsense observation was translated, improperly as we now know, into the creationist taxonomy of Linnaeus. The great Swedish naturalist regarded species as God's created entities, and he gathered them together into genera, genera into orders, and orders into classes, to form the taxonomic hierarchy that we all learned in high school (several more categories, families and phyla, for example, have been added since Linnaeus's time). The creationist version reached its apogee in the writings of America's greatest nineteenth-century naturalist (and last truly scientific creationist), Louis Agassiz. Agassiz argued that species are incarnations of separate ideas in God's mind, and that higher categories (genera, orders, and so forth) are therefore maps of the interrelationships among divine thoughts. Therefore, taxonomy is the most important of all sciences because it gives us direct insight into the structure of God's mind.

Darwin changed this reverie forever by proving that species are related by the physical connection of genealogical descent. But this immensely satisfying resolution for the great puzzle of nature's order engendered a subsidiary problem that Darwin never fully resolved: If all life is interconnected as a genealogical continuum, then what reality can species have? Are they not just arbitrary divisions

ILLUSTRATIONS BY ALAN E. COBER

of evolving lineages? And if so, how can the bugs in my backyard be ordered in separate units? In fact, the two greatest evolutionists of the nineteenth century, Lamarck and Darwin, both questioned the reality of species on the basis of their evolutionary convictions. Lamarck wrote, "In vain do naturalists consume their time in describing new species"; while Darwin lamented: "we shall have to treat species as . . . merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term *species*" (from the *Origin of Species*).

Fig 1

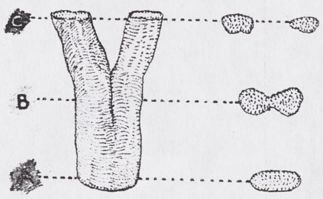


Figure 1. Species go through a period of ambiguity while a new branch is forming (B), and then become clearly separate (C).

But when we examine the technical writings of both Lamarck and Darwin, our sense of paradox is heightened. Darwin produced four long volumes on the taxonomy of barnacles, using conventional species for his divisions. Lamarck spent seven years (1815–1822) publishing his generation's standard, multivolume compendium on the diversity of animal life—*Histoire naturelle des animaux sans vertèbres*, or *Natural History of Invertebrate Animals*—all divided into species, many of which he named for the first time himself. How can these two great evolutionists have denied a concept in theory and then used it so centrally and extensively in practice? To ask the question more generally: If the species is still a useful and necessary concept, how can we define and justify it as evolutionists? ①

FIG. 2

Figure 2. The time of ambiguity at the origin of the new species (B) from a parental line (A) is relatively short. ②

The solution to this question requires a preamble and two steps. For the preamble, let us acknowledge that the conceptual problem arises when we extend the "bugs in my backyard" example into time and space. A momentary slice of any continuum looks tolerably discrete; a slice of salami or a cross section of a tree trunk freezes a complexly changing structure into an apparently stable entity. Modern horses are discrete and separate from all other existing species, but how can we call the horse (*Equus caballus*) a real and definable entity if we can trace an unbroken genealogical series back through time to a dog-size creature with several toes on each foot? Where did this "dawn horse," or "eohippus," stop and the next stage begin; at what moment did the penultimate stage become *Equus caballus*? I now come to the two steps of an answer.

First, if each evolutionary line were like a long salami, then species would not be real and definable in time and space. But in almost all cases large-scale evolution is a story of branching, not of transformation in a single line—bushes, not ladders, in my usual formulation. A branch on a bush is an objective division. One species rarely turns into another by total transformation over its entire geographic range. Rather, a small population becomes geographically isolated from the rest of the species—and this fragment changes to become a new species while the bulk of the parental population does not alter. "Dawn horse" is a misnomer because rhinoceroses evolved from the same parental lineage. The lineage split at an objective branching point into two lines that became (after further events of splitting) the great modern groups of horses (eight species, including asses and zebras) and rhinos (a sadly depleted group of formerly successful species).

Failure to recognize that evolution is a bush and not a ladder leads to one of the most common vernacular misconceptions about human biology. People often challenge me: "If humans evolved from apes, why are apes still around?" To anyone who understands the principle of bushes, there simply is no problem: the human lineage emerged as a branch, while the rest of the trunk continued as apes (and branched several more times to yield modern chimps, gorillas, and so on). But if you think that evolution is a ladder or a salami, then an emergence of humans from apes should mean the elimination of apes by transformation.

Second, you might grasp the principle of bushes and branching but still say: Yes, the ultimate products of a branch become objectively separate, but early on, while the branch is forming, no clear division can be made, and the precursors of the two species that will emerge must blend indefinably (figure 1). And if evolution is gradual and continuous, and if most of a species' duration is spent in this state of incipient formation, then species will not be objectively definable during most of their geologic lifetimes.

Fair enough as an argument, but the premise is wrong. New species do (and must) have this period of initial ambiguity. But species emerge relatively quickly, compared with their period of later stability, and then live for long periods—often millions of years—with minimal change (figure 2). Now, suppose that on average (and this is probably a fair estimate), species spend one percent of their geologic lifetimes in this initial state of imperfect separation. Then, on average, about one species in a hundred will encounter problems in definition, while the other 99 will be discrete and objectively separate—cross sections of branches showing no confluence with others (C, figure 1). Thus, the principle of bushes, and the speed of branching, resolve the supposed paradox: continuous evolution can and does yield a world in which the vast majority of species are separate from all others and clearly definable at any moment in time. Species are nature's objective packages.

I have given a historical definition of species—as unique and separate branches on nature's bush. We also need a functional definition, if only because historical evidence (in the form of a complete fossil record) is usually unavailable. The standard criterion, in use at least since the days of the great French naturalist Georges de Buffon (a contemporary of Linnaeus), invokes the capacity for interbreeding. Members of a species can breed with others in the same species but not with individuals belonging to different species.

This functional criterion is a consequence of the historical definition: distinct separateness of a branch emerges only with the attainment of sufficient evolutionary distance to preclude interbreeding, for otherwise the branch is not an irrevocably separate entity and can amalgamate with the parental population. Exceptions exist, but the reproductive criterion generally works well and gives rise to the standard one-liner for a textbook definition of a species: "a population of actually or potentially reproducing organisms sharing a common gene pool."

MUCH OF THE ORDINARY ACTIVITY of evolutionary biologists is devoted to learning whether or not the groups they study are separate species by this criterion of "reproductive isolation." Such separateness can be based on a variety of factors, collectively termed "isolating mechanisms": for example, genetic programs so different that an embryo cannot form even if egg and sperm unite; behaviors that lead members of one species to shun individuals from other populations; even something so mundane as breeding at different times of the year, or in different parts of the habitat—say, for example, on apple trees rather than on plum trees—so that contact can never take place. (We exclude simple geographic separation—living on different continents, for example—because an isolating mechanism must work when actively challenged by a potential for interbreeding through spatial contact. I do not belong to a separate species from my brethren in Brazil just because I have never been there. Similarly, reproductive isolation must be assessed by ordinary behavior in a state of nature. Some truly separate species can be induced to interbreed in zoos and laboratories. The fact that zoos can make tiglons—tiger-lion hybrids—does not challenge the separate status of the two populations as species in nature.)

FIG. 3

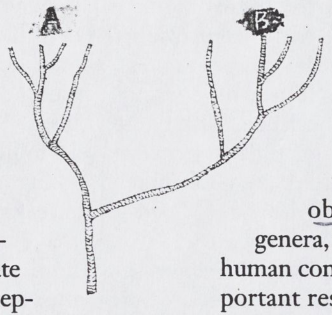


Figure 3. Branches are objective species. But the clusters they form (A and B) are classified partly according to human conventions.

Modern humans (species *Homo sapiens*) fit these criteria admirably. We are now spread all over the world in great numbers, but we began as a little twig in Africa (the historical criterion). We may look quite different from one another in a few superficially striking aspects of size, skin color, and hair form, but there is astonishingly little overall genetic difference among our so-called races. Above all (the functional criterion), we can all interbreed with one another (and do so with avidity, always, and all over the world), but not with any member of another species (movies about flies notwithstanding). We are often reminded, quite correctly, that we are very similar in overall genetic program to our nearest cousin, the chimpanzee—but no one would mistake a single individual of either species, and we do not hybridize (again, various science fictions notwithstanding).

I do not say that these criteria are free from exceptions; nature is nothing if not a domain of exceptions, where an example against any clean generality can always be found. Some distinct populations of plants, for example, can and frequently do interbreed with others that ought to be separate species by all other standards. (This is why the classification of certain groups—the rhododendrons, for example—is such a mess.) But the criteria work in the vast majority of cases, including humans. Species are not arbitrary units, constructed for human convenience, in dividing continua. Species are the real and objective items of nature's morphology. They are "out there" in the world as historically distinct and functionally separate populations "with their own historical role and tendency" (as the other textbook one-liner proclaims).

Species are unique in the Linnaean hierarchy as the only category with such objectivity. All higher units—genera, families, phyla, et cetera—are human conventions in the following important respect. The evolutionary tree itself is objective; the branches (species) emerge, grow, and form clusters by subsequent branching. The clusters (figure 3) are clearly discernible. But the status we award to these so-called higher taxa (clusters of branches with a single root of common evolutionary ancestry) is partly a matter of human decision. Clusters A and B in the figure are groups of species with a common parent. Each

Oncorhy
Salmo
Parasalmo

Oregonichthys – Deshutes
– Umpqua
not far
enough – bouvieri

branch in each cluster is an objective species. But what are the clusters themselves? Are they two genera or two families? Our decision on this question is partly a matter of human preference constrained by the rules of logic and the facts of nature. (For example, we cannot take one species from cluster A and one from cluster B and put them together as a single genus—for this would violate the rule that all members of a higher taxon must share a common ancestor without excluding other species that are more closely related to the common ancestor. We cannot put domestic cats and dogs in one family while classifying lions and wolves in another.)

Int. Rules

The taxonomic hierarchy recognizes only one unit below species—the subspecies. Like higher taxa, subspecies are also partly objective but partly based on human decision. Subspecies are defined as distinctive subpopulations that live in a definite geographic subsection of the entire range of the species. I cannot, for example, pluck out all tall members of a species, or all red individuals, wherever they occur over the full geographic range, and establish them as subspecies. A subspecies must be a distinct geographic subpopulation—not yet evolved far enough to become a separate species in its own right but different enough from other subpopulations (in terms of anatomy, genetic structure, physiology, or behavior) that a taxonomist chooses to memorialize the distinction with a name. Yet subspecies cannot be irrevocably unique natural populations (like full species) for two reasons: First, the decision to name them rests with human taxonomists, and isn't solely dictated by nature. Second, they are, by definition, still capable of interbreeding with other subpopulations of the species and are, therefore, impermanent and subject to reamalgamation.

Rules
subsp.

~~polytopic~~
f[illegible]
traits
[illegible]
polyphyletic
[illegible]
[illegible]

– Resoth. E.S.A. – subsp. – pop.

THIS DIFFERENCE BETWEEN SPECIES and subspecies becomes important in practice because our Endangered Species Act currently mandates the protection of subspecies as well. I do not dispute the act's intention or its teeth, for many subspecies do manifest distinctly evolved properties of great value and wonder (even if these properties do not render them reproductively isolated from other populations of the species). We would not, after all, condone the genocide of all Caucasian human beings because members of other races would still exist; human races, if formally recognized at all, are subspecies based on our original geographic separations. But since subspecies do not have the same objective status as species (and since not all distinct local populations bear separate names), argument over what does and does not merit protection is inevitable. Most of the major ecological wrangles of recent years—rows over the Mount Graham red squirrel or the Northern spotted owl—involve subspecies, not species.

gene flow

These taxonomic issues were once abstract, however important. They are now immediate and vital—and all educated people must understand them in the midst of our current crisis in biodiversity and extinction. I therefore close with two observations.

By grasping the objective status of species as real units in nature (and by understanding why they are not arbitrary divisions for human convenience), we may better comprehend the moral rationale for their preservation. You can expunge an arbitrary idea by rearranging your conceptual world. But when a species dies, an item of natural uniqueness is gone forever. Each species is a remarkably complex product of evolution—a branch on a tree that is billions of years old. All the king's horses and men faced an easy problem compared with what we would encounter if we tried to reconstitute a lost species. Reassembling Humpty-Dumpty is just an exceedingly complex jigsaw puzzle, for the pieces lie at the base of the wall. There are no pieces left when the last dodo dies.

But all species eventually die in the fullness of geologic time, so why should we worry? In the words of Tennyson (who died exactly 100 years ago, so the fact is no secret):

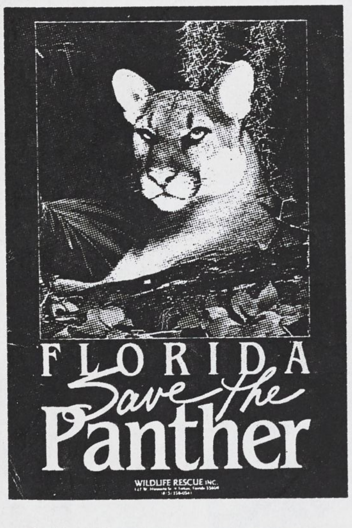
> From scarped cliff and quarried stone
> She cries, "A thousand types are gone:
> I care for nothing. All shall go."
> (From *In Memoriam.*)

The argument is true, but the time scale is wrong for our ethical concerns. We live our lives within geologic instants, and we should make our moral decisions at this proper scale—not at the micromoment of thoughtless exploitation for personal profit and public harm; but not at Earth's time scale of billions of years either (a grand irrelevancy for our species' potential tenure of thousands or, at most, a few million years).

We do not let children succumb to easily curable infections just because we know that all people must die eventually. Neither should we condone our current massive wipeout of species because all eventually become extinct. The mass extinctions of our geologic past may have cleared space and created new evolutionary opportunity—but it takes up to 10 million years to reestablish an interesting new world, and what can such an interval mean to us? Mass extinctions may have geologically distant benefits, but life in the midst of such an event is maximally unpleasant—and that, friends, is where we now reside, I fear.

Species are living, breathing items of nature. We lose a bit of our collective soul when we drive species (and their entire lineages with them), prematurely and in large numbers, to oblivion. Tennyson, paraphrasing Goethe, hoped that we could transcend such errors when he wrote, in the same poem:

> I held it truth, with him who sings
> To one clear harp in divers tones
> That men may rise on stepping-stones
> Of their dead selves to higher things. ◻



POLICY FORUM

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.

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.

tuna

short term

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

(*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.

J.W. Powell
west
water

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*).

best

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.

4

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.

– hutcherson

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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19. We thank D. Schluter, L. Gass, and L. Rowe for helpful comments. Our research was supported in part by the Natural Sciences and Engineering Research Council of Canada under grants A9239 and A5869 and by a State of Washington Sea Grant.

Proc. Natl. Acad. Sci. USA
Vol. 90, pp. 6995–6999, August 1993
Genetics

Determination of the phylogenetic relationships among Pacific salmonids by using short interspersed elements (SINEs) as temporal landmarks of evolution

(retroposon/PCR/phylogeny/orthologous locus/salmon)

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Communicated by C. Clark Cockerham, March 31, 1993 (received for review November 20, 1992)

Bob –
Nakano sent me this.
Can you provide a citation?
Also attached copy is
yours to keep.
KDF

ABSTRACT **Several subfamilies of the salmonid *Hpa* I short interspersed element (SINE) family were isolated from salmonid genomes and were sequenced. For each genomic locus that represented the subfamily, amplification by PCR of the orthologous loci in the 12 fish allowed us to determine the order of branching of the Pacific salmonid species. The deduced phylogeny suggests three evolutionary lines, namely, a line of chum salmon, pink salmon, and kokanee; a line of coho salmon and chinook salmon; and a line of steelhead trout. Our data also support a change in the phylogenetic assignment of steelhead trout from *Salmo* to *Oncorhynchus*. We present here an extensive phylogenetic tree constructed from an analysis of differential insertion of SINEs, and we propose that SINE insertion analysis is one of the best available methods for clarifying the order of divergence of closely related species.**

A retroposon is defined as a nucleotide sequence, present initially as a cellular RNA transcript, that has been reincorporated into the genome, presumably via a cDNA intermediate. Retroposons constitute roughly 10% of the human genome and are similarly abundant in other mammalian genomes (1, 2). As a result, the remarkable fluidity of eukaryotic genomes reflects the contributions of retroposition (2) as well as mechanisms operating at the DNA level such as mutation and recombination (1–4). Retroposons can be unique to one species, a few species, a genus, or in some cases a family. Retroposition is therefore a specialized form of gene duplication, which is believed to be of major importance in the creation of genetic diversity during evolution (5).

Nonviral retroposons are classified into three main groups: processed retropseudogenes, LINEs (long interspersed elements), and SINEs (short interspersed elements) (6). Except for the rodent type 1 and human *Alu* families (7, 8), all of the SINE families examined to date have been shown to be derived from tRNAs (9–14). In contrast to DNA transposable elements, which are often capable of being excised precisely, SINEs appear to be inserted irreversibly and should therefore provide an ideal evolutionary and phylogenetic marker (4).

The Pacific salmon and trout (*Oncorhynchus*) are a group of closely related species with complex life histories and an interesting global distribution (reviewed in ref. 15). Previously, in an attempt to elucidate a possible role of SINEs in the genomic organization and speciation of salmonids, we characterized three families of tRNA-derived SINEs in salmonid genomes (16, 17). The salmon *Sma* I family is restricted to the genomes of chum salmon and pink salmon. The charr *Fok* I family is present only in species that belong to the genus *Salvelinus*. The third family, the salmonid *Hpa* I family, is present in all species in the family Salmonidae but not in other species (16). SINEs were amplified sp lineages during evolution.

Our data prompted us to attempt to construct a phylogenetic tree for the salmonid species by using SINE insertions as irreversible events that would serve as informative markers of evolution. In this report, we present a characterization of the four subfamilies of the *Hpa* I family.[†] These subfamilies were amplified in the four different ancestral species within the genus *Oncorhynchus*. Such characterization provides a highly reliable order of branching of the various species of *Oncorhynchus*.

MATERIALS AND METHODS

Experiments were performed by using standard techniques (18–21).

The fish species examined in this study and their geographic sources are listed in Table 1. The family Salmonidae consists mainly of four genera: *Oncorhynchus*, *Salmo*, *Salvelinus*, and *Hucho*. The genus *Oncorhynchus* includes eight species, of which six species were analyzed in this study. Genomic DNAs from chum salmon (*O. keta*), kokanee (*O. nerka adonis*), and coho salmon (*O. kisutch*) were used to construct three genomic libraries. Each genomic library was screened for phage clones that contained the salmonid *Hpa* I family and their sequences were determined by the chain-termination method (19). When a unit of the family appeared to be integrated into a unique region of the genome, we synthesized 5′ and 3′ 20-meric primers that flanked the unit. Then PCR was performed (20), using the DNAs from the 12 listed species as templates. Each locus was named after the number of the clone and the name of the species from which it was isolated. For example, when a phage clone was isolated from the genomic library of kokanee and the number of the clone was 345, the locus was named Hpa(ON)-345 (where ON stands for *O. nerka*). The orthologous loci of chum salmon (*O. keta*), pink salmon (*O. gorbuscha*), coho salmon (*O. kisutch*), and steelhead trout (*O. mykiss*), which could be detected by PCR, were named Hpa(OK)-345, Hpa(OG)-345, Hpa(OKi)-345, and Hpa(OMy)-345, respectively. To confirm the presence or absence of a SINE unit, Southern hybridization experiments were performed (21) and several sequences of products of PCR at the orthologous loci were determined. To distinguish different loci from one another, different numbering systems were adopted for the different genomic libraries.

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Abbreviation: SINE, short interspersed element.

*To whom reprint requests should be sent at the present address: Faculty of Bioscience and Biotechnology, Tokyo Institute of Technology, 4259 Nagatsuta-cho, Midori-ku, Yokohama 227, Japan.

[†] The sequences reported in this paper have been deposited in the GenBank data base (accession nos. D16238–D16246).

Proc. Natl. Acad. Sci. USA
Vol. 90, pp. 6995–6999, August 1993
Genetics

Determination of the phylogenetic relationships among Pacific salmonids by using short interspersed elements (SINEs) as temporal landmarks of evolution

(retroposon/PCR/phylogeny/orthologous locus/salmon)

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Communicated by C. Clark Cockerham, March 31, 1993 (received for review November 20, 1992)

ABSTRACT **Several subfamilies of the salmonid *Hpa* I short interspersed element (SINE) family were isolated from salmonid genomes and were sequenced. For each genomic locus that represented the subfamily, amplification by PCR of the orthologous loci in the 12 fish allowed us to determine the order of branching of the Pacific salmonid species. The deduced phylogeny suggests three evolutionary lines, namely, a line of chum salmon, pink salmon, and kokanee; a line of coho salmon and chinook salmon; and a line of steelhead trout. Our data also support a change in the phylogenetic assignment of steelhead trout from *Salmo* to *Oncorhynchus*. We present here an extensive phylogenetic tree constructed from an analysis of differential insertion of SINEs, and we propose that SINE insertion analysis is one of the best available methods for clarifying the order of divergence of closely related species.**

A retroposon is defined as a nucleotide sequence, present initially as a cellular RNA transcript, that has been reincorporated into the genome, presumably via a cDNA intermediate. Retroposons constitute roughly 10% of the human genome and are similarly abundant in other mammalian genomes (1, 2). As a result, the remarkable fluidity of eukaryotic genomes reflects the contributions of retroposition (2) as well as mechanisms operating at the DNA level such as mutation and recombination (1–4). Retroposons can be unique to one species, a few species, a genus, or in some cases a family. Retroposition is therefore a specialized form of gene duplication, which is believed to be of major importance in the creation of genetic diversity during evolution (5).

Nonviral retroposons are classified into three main groups: processed retropseudogenes, LINEs (long interspersed elements), and SINEs (short interspersed elements) (6). Except for the rodent type 1 and human *Alu* families (7, 8), all of the SINE families examined to date have been shown to be derived from tRNAs (9–14). In contrast to DNA transposable elements, which are often capable of being excised precisely, SINEs appear to be inserted irreversibly and should therefore provide an ideal evolutionary and phylogenetic marker (4).

The Pacific salmon and trout (*Oncorhynchus*) are a group of closely related species with complex life histories and an interesting global distribution (reviewed in ref. 15). Previously, in an attempt to elucidate a possible role of SINEs in the genomic organization and speciation of salmonids, we characterized three families of tRNA-derived SINEs in salmonid genomes (16, 17). The salmon *Sma* I family is restricted to the genomes of chum salmon and pink salmon. The charr *Fok* I family is present only in species that belong to the genus *Salvelinus*. The third family, the salmonid *Hpa* I family, is present in all species in the family Salmonidae but not in other species (16). These results suggest that these SINEs were amplified specifically within certain salmonid lineages during evolution.

Our data prompted us to attempt to construct a phylogenetic tree for the salmonid species by using SINE insertions as irreversible events that would serve as informative markers of evolution. In this report, we present a characterization of the four subfamilies of the *Hpa* I family.† These subfamilies were amplified in the four different ancestral species within the genus *Oncorhynchus*. Such characterization provides a highly reliable order of branching of the various species of *Oncorhynchus*.

MATERIALS AND METHODS

Experiments were performed by using standard techniques (18–21).

The fish species examined in this study and their geographic sources are listed in Table 1. The family Salmonidae consists mainly of four genera: *Oncorhynchus*, *Salmo*, *Salvelinus*, and *Hucho*. The genus *Oncorhynchus* includes eight species, of which six species were analyzed in this study. Genomic DNAs from chum salmon (*O. keta*), kokanee (*O. nerka adonis*), and coho salmon (*O. kisutch*) were used to construct three genomic libraries. Each genomic library was screened for phage clones that contained the salmonid *Hpa* I family and their sequences were determined by the chain-termination method (19). When a unit of the family appeared to be integrated into a unique region of the genome, we synthesized 5′ and 3′ 20-meric primers that flanked the unit. Then PCR was performed (20), using the DNAs from the 12 listed species as templates. Each locus was named after the number of the clone and the name of the species from which it was isolated. For example, when a phage clone was isolated from the genomic library of kokanee and the number of the clone was 345, the locus was named Hpa(ON)-345 (where ON stands for *O. nerka*). The orthologous loci of chum salmon (*O. keta*), pink salmon (*O. gorbuscha*), coho salmon (*O. kisutch*), and steelhead trout (*O. mykiss*), which could be detected by PCR, were named Hpa(OK)-345, Hpa(OG)-345, Hpa(OKi)-345, and Hpa(OMy)-345, respectively. To confirm the presence or absence of a SINE unit, Southern hybridization experiments were performed (21) and several sequences of products of PCR at the orthologous loci were determined. To distinguish different loci from one another, different numbering systems were adopted for the different genomic libraries.

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4-7-94

Ecological Applications Vol 3 N4
Nov 1993

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Forum

Science and sustainability[1]

No term receives more attention in discussions of environmental management than "sustainability." On the other hand, perhaps no term is less well understood, even though sustainability was the keystone concept in the Ecological Society of America's Lubchenco report (Lubchenco et al. 1991), and provided the basis for the catchy title "Sustainable Biosphere Initiative." Is sustainability a well-defined concept? Is it an appropriate goal for management? And if it is, does human avarice make its realization impossible? Are limitations to achieving sustainability based on our lack of knowledge of what needs to be done, or are any such limitations sociological in origin? Is a goal of sustainability a call for more basic research, or are such calls self-serving and irrelevant?

In a provocative and thoughtful paper (Ludwig et al. 1993), reprinted here from *Science,* Ludwig, Hilborn, and Walters argue that claims that "basic research will . . . 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." Because of the importance of the issues addressed by Ludwig et al. and the attention that the paper drew (e.g., Stevens 1993), I invited the authors to elaborate on their ideas in the pages that follow, and simultaneously invited a distinguished group of ecologists and environmental scientists to comment on the original paper. None of the commentators saw the contributions of others, except to the extent that they may have shared them among themselves. Only the original *Science* article, and not the extended versions, were sent to the Forum participants.

Expecting a limited response to my invitation, I was happily overwhelmed with contributions, representing a diversity of opinions. Obviously, the issues addressed were very much on the minds of more people than I realized. Although there are necessarily considerable overlaps among the responses, there hardly is convergence. As should be expected, different aspects of the *Science* article attracted the attention of different commentators, most finding points of agreement as well as points of disagreement. The collection as a whole makes for fascinating reading, and a valuable addition to *Ecological Applications.* The success of this effort surely will encourage us to continue the tradition of seeking a broad spectrum of views on issues at the cutting edge of ecological management.

The notion of sustainability is a vague and elusive one, and attention must be directed to what it means before asking whether and how it might be achieved. Solow (1991) argues that "Sustainability as a moral obligation is a general obligation not a specific one." By this, he means that the substitutability of one resource for another must be considered, both because sustainable use of nonrenewable resources is an impossibility, and because the ultimate goal should be simply to "leave to the future the option or the capacity to be as well off as we are." That does not require a reductionistic attention to maintaining each species or resource at a constant level, but a broader attention to more general goals (see also Holling's paper in this Forum). Thus, the question of the degree to which one can extrapolate from the management of particular fisheries, for example, is called into question. What sustainability does require, however, is attention to the management of systems under uncertainty, to the linkages among physical, biological, and socioeconomic systems, and to the interface between science and policy (Huntley et al. 1991, Levin 1992, Ludwig et al. 1993). It further requires (e.g., Solow 1991) that we confront the trade-offs between intergenerational equity, the justification usually given for sustainability, and intragenerational equity. The latter requires us to address the need not only for people in developing nations, but also for disadvantaged groups within developed nations, to reap the fruits of the environment sufficiently for them to experience life in ways comparable to what most of us enjoy. Solow (1991) argues ". . . there is something faintly phony about deep concern for the future combined with callousness about the state of the world today." Finally, and most fundamentally, achieving sustainability requires

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[1] Reprints of this 45-page Forum are available for $7.00 each. Order reprints from the Business Manager, Ecological Society of America, Arizona State University, Box 873211, Tempe, AZ 85287-3211.

the consideration of problems of population growth, and the linkages between growth and environmental degradation. As Solow points out, population growth is the by-product of old-age insurance policies of a special form most appropriate for developing countries: having children who can take care of their aged parents. There seems little doubt that more research is needed into sustainability, including basic research into ecological and socioeconomic systems, but we must not delude ourselves into believing that the issues are entirely scientific, or even primarily scientific. What is needed are mechanisms for performing the science that will guide society in making its decisions, and for building bridges between science and decision making.

Needless to say, the papers in this Forum will not put the issue of sustainability to rest; hopefully, however, they will help to inform the debate on what is, arguably, the central environmental issue facing us.

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S. A. LEVIN

Uncertainty, Resource Exploitation, and Conservation: Lessons from History[1]

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.

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 rec-

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[1] Reprinted by permission from *Science* 260:17, 36 (2 April 1993). © AAAS.

ord 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 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 un-

specified 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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19. We thank D. Schluter, L. Gass, and L. Rowe for helpful comments. Our research was supported in part by the Natural Sciences and Engineering Research Council of Canada under grants A9239 and A5869 and by a State of Washington Sea Grant.

Ecological Applications, 3(4), 1993, pp. 550–552

THE LIMITS OF APPLIED ECOLOGICAL RESEARCH[1,2]

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In our article in *Science* (Ludwig et al. 1993), we challenged the assumption that ecological research is the most productive avenue to determining the limits of sustainability in natural resource management. We argued that there will always be major uncertainties in how ecological systems will respond to management actions and that society must make important decisions in the face of such uncertainty. Politicians, resource managers, and user groups should not, and cannot, look to more ecological research as the primary tool to tell them what to do. This argument is built on three elements: first, the rate of learning about ecological systems is slow enough that waiting for better scientific knowledge to provide iron-clad answers is futile; second, decisions have to be made now, given current knowledge; and finally, in many resource systems the only way to learn about their sustainability is to exploit them.

The editor of *Ecological Applications* has kindly offered us the opportunity to elaborate on some of these ideas. In this brief note we would like to expand on the limits of applied ecological research from the perspective of a former ecologist who has been working primarily in the management of exploited resources for 20 yr.

For many years we suffered from an acute case of physics envy. One of us (R. Hilborn) did his Ph.D. research on population cycles with Charles Krebs, who had done his work with Dennis Chitty, who had done his work with Charles Elton. It was quite discouraging to look back on >60 yr of field experimentation on mice, voles, hares, etc., and realize how little progress had been made in understanding these population cycles when compared with the progress in physics, chemistry, genetics, and a host of other fields. We believe that while most ecologists will admit that progress has indeed been slow, few fully appreciate why this is so.

Platt (1964) provided one possible explanation for the difference in rates of progress. He argued that the fields that made rapid progress did so because of a rigorous experimental method that designed critical experiments and quickly distinguished between competing hypotheses. Krebs and Chitty were among the leading practitioners of experimental ecology, and yet it did not seem to us that the rate of progress in their type of ecology was rapidly outpacing other aspects of ecology less committed to experimental testing of hypotheses, nor did small mammal research seem to keep up with the fast-paced fields outside of ecology. Hilborn and Stearns (1978) argued that the critical testing of hypotheses performed in small mammal research had erred in testing single-factor hypotheses in isolation. While we still find that the ideas in Platt and Hilborn and Stearns are valid, we think the differential rates of progress can be ascribed to a simpler fact. Ecology is a more difficult science than physics, chemistry, genetics, or physiology!

The reason ecology is more difficult is plain: experiments take longer, replication, control, and randomization are harder to achieve, and ecological systems have the nasty habit of changing over time. We don't think that the problem with ecology is the inherent complexity of the systems under study. A human body or a single cell are very complex systems too, and yet progress in medical research has been made at an astounding pace.

Our contention is that the rate of progress in a field of science will be largely governed by how quickly hypotheses can be tested, how many replicates can be performed, how good the controls can be, and whether experimental treatments can be randomized. All other things being equal, a field that can perform an experiment in a week will make progress 52 times faster than a field where an experiment takes a year. If one compares experiments on small mammal cycles that take 3–4 yr with molecular biology experiments that may take a few weeks, it is no surprise that molecular biology makes staggering progress compared with small mammal research.

Replication is perhaps the most important element in the scientific method. A major part of a scientific paper is providing enough description of methods so that someone else can replicate it. If others cannot replicate our results, our findings are not likely to be widely accepted. Most field experimentation in ecology takes a few years. Allowing for publication time, few field experiments are likely to be performed, published, and replicated in much less than a decade. Again, compare this to molecular biology where experiments are

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

often described in preprints sent by FAX or e-mail, and repeated in a matter of weeks.

Replication poses even greater problems when working on the question of sustainability in natural resources. In many cases there is only a single resource and the time scale of the system is on the order of decades. Consider the time scale of experimentation and replication for issues like old-growth forest, marine mammals, or global climate change.

The second key element of experimental science is controls. For many natural resources controls are difficult if not impossible to obtain, and even when available, they are rarely perfect. In the absence of controls, experiments are more ambiguous and learning will be slower. In laboratory systems the optimum sample size is determined by budget; it is always better to have more test tubes. But in ecological field research no two systems are identical, and the larger your sample size, the more internally heterogeneous the controls will be. The optimum sample size is a balance between increasing numbers and increasing internal heterogeneity, and it may be only 2 or 3. When you have few replicates and controls, the results of any experiment are more ambiguous than when you have many replicates and controls. Progress will be faster in a field where replicates and controls are more abundant than in a field (ecology) where they are scarce.

Ecologists often rely on natural experiments to understand the dynamics of ecosystems. These experiments may be human-induced changes such as fish harvesting or oil spills, or may be natural events such as fire. Such natural perturbations provide a much weaker form of experimental evidence than planned experiments because we have no assurance that the treatments were applied at random with respect to naturally occurring differences between sites. The Exxon Valdez Oil Spill provided enormous funds (by ecological standards) for study of a perturbed ecosystem, yet many studies that found differences between oiled and unoiled sites could not determine if the differences were pre-existing. Oil did not strike at random, and it is possible that many of the differences seen between oiled and unoiled sites were correlated with the physical factors that determined if a beach was hit by oil or spared to begin with.

Ecologists have recognized that progress will be more rapid if you work on a small, short-lived species rather than on a large, long-lived one, and many ecologists can perform experiments and replicate them in a matter of weeks or months. Unfortunately, the key issues of sustainability generally revolve around large systems and large animals where the problems of replication, control, and randomization mentioned above are most acute. Further, the only way to understand the sustainability of many systems is to exploit them. If you want to understand how much yield can be taken from a population, you have to exploit it. Certainly, ecological knowledge of the age distribution and reproductive biology will give you an idea of the range of potential yield, but if you want to try to maximize yield, you have got to harvest. Indeed, if you want to find the maximum potential harvest, you have to go through a period of overexploitation (Hilborn and Walters 1992). In many resource management systems, each problem is unique enough that you have to learn about its sustainability by systematically and experimentally harvesting from it. Ecological research cannot tell managers how much yield to take: it can only guide the managers in a well-planned management program, and such a program will of necessity entail risks. The current view, which we criticized in our paper, is that ecological research can substantially reduce these risks.

A final difficulty of ecological systems is that they change over time. What we learn in one decade may not be true in the next. As we have come to better understand fluctuations in fish stocks, we find many cases where the entire underlying basis of fish production changes periodically. Cushing (1982) has shown that the herring yield in Norway and Sweden has undergone periodic, half-century scale fluctuations for several hundred years. Recent salmon yields in Alaska are at record levels, and it is believed that these yields are the result of a major oceanographic change that occurred in the late 1970s. What was learned about the sustainability of harvest from these Alaska salmon stocks up to the late 1970s has been, of necessity, largely discarded. What we knew in 1975 is of little use today. We may design a program to learn about the sustainable yield, but by the time the data are collected and we think we know how the system responds to exploitation, it will have changed and our data are obsolete. The key question is whether we can design research programs that will learn about a system faster than the system changes.

The preceding discussion explains why we believe learning about ecological systems is, necessarily, much slower than learning about molecular biology or physiology, and why ecologists cannot be expected to, nor should they claim to be able to, provide decision makers with the definitive answer after ever more research. Rather ecologists need to be aware of the limits of their science so as not to create unrealistic expectations.

In many areas of sustainability, ecologists have become significant technical advisors and advocates. Unfortunately, they are poorly prepared for this task. There is a great difference between the way science is normally practiced and the way decision makers should go about their business. Rational decision making requires that one balance the risks and benefits of a variety of possible outcomes. The most effective action is often one that is robust to a variety of possible states of the world. It is seldom achieved by optimizing after fixing upon a single best estimate or most likely state of the world.

A first step in rational decision making is to assess the relative plausibility (probability) of a variety of parametric hypotheses, given the data available. Such an assessment is awkward using standard frequentist statistical methods, since they are concerned with the properties of functions of the data (such as means and standard errors) if data are sampled repeatedly. In ecological decision problems, data are not sampled repeatedly: we must work with what we have. Frequentist methods cannot answer questions concerning the relative probabilities of various parameter values since parameters are fixed, not random. Similarly, hypotheses are either true or false: one cannot assign a probability to a hypothesis using frequentist methods. The result of statistical hypothesis testing methods is typically a single favored hypothesis. This leads to decision making that ignores uncertainty in our knowledge and consequently neglects the consequences of unlikely events with bad outcomes. Often economic optimization models (such as the maximum sustained yield for fisheries) are applied to attempt to maximize yields even though the data provide little information about biological characteristics of the exploited stocks. The consequence of such decision making is a continual series of surprises and failures.

In contrast, the modern theory of decision (Chernoff and Moses 1959, Berger 1985, Lindley 1985, Mangel 1985) is based upon the subjective interpretation of probability. Probabilities are used to quantify degrees of belief in a variety of hypotheses. The main tool is Bayes' theorem, which enables one to update estimates as new data are available. The first product of such an analysis is a probability distribution for the various hypotheses, calculated from the data that are currently available. On the basis of this distribution one can assess the probable consequences of a variety of actions. The action that is recommended can be chosen on its aggregated performance under a variety of plausible hypotheses. An important component of this process is the careful description of uncertainties in our present knowledge. One can often design experiments that will reduce such uncertainties in the future. There is no substitute for informative data and careful experiments. The advantage of decision-theoretic methods is that uncertainty is handled in a consistent and systematic way rather than being ignored as a consequence of an hypothesis test.

None of the above discussion suggests we should not do ecological research. Rather it suggests that ecological research on large-scale systems of interest in most discussions of sustainability has limitations. Ecology has made a lot of progress and we are not embarrassed to say that we are ecologists to our colleagues in physics and chemistry. Rather we take pride in the intrinsic difficulty of the field and tell them "Rocket scientists have it easy!" However, when providing society with advice about the sustainability of natural resource use, we keep in mind the explosion of the space shuttle Challenger. If rocket scientists can make such a big mistake, we ecologists, working in a much harder field, need to be aware of the limitations of our understanding.

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Ecological Applications, 3(4), 1993, pp. 552–555

INVESTING IN RESEARCH FOR SUSTAINABILITY[1,2]

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Is sustainable use of a living resource impossible, sustainable development an oxymoron, and scientific research of limited utility in designing policies and managing resource exploitation? That is what Ludwig et al. (1993) seem to suggest in their article on the history of exploitation of renewable resources. They are probably correct if sustainable use or sustainable development is defined as the first phase of exploitation of a single species and science as small-scale reduc-

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[1] Manuscript received 2 June 1993.

[2] For reprints of this Forum, see footnote 1, p. 545.

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Diversity

How to Lie with Biodiversity

Biodiversity is the bandwagon of the moment. Unfortunately, the concept is sufficiently complex that almost any population biology study, with almost any conclusion, can be framed as an effort to measure or conserve biodiversity. Based on what I have seen in the literature and heard at recent scientific meetings, here is a primer on some of the more popular ways to bend biodiversity data.

Suppose you wish to claim that a species is disappearing. With the explanation that time and funding were limited, you might present population trajectories based on as few as two estimates of abundance. Perhaps the final abundance estimate was obtained during a drought year. Use a technique for estimating abundance that has untested assumptions. Avoid stating confidence limits. Under these conditions a coin toss would suggest that about half of the species should show declines. If yours does, publish.

If it does not, find a post hoc explanation to account for the result. For example, hypothesize that dry weather reduced or increased activity and distorted your counts. Give your conclusion some statistical rigor by correlating weather phenomena with measures of abundance. But of course don't test the weather hypothesis against an independent data set.

Once you have a hypothesis to account for the apparent influence of weather on abundance, you're all set to model the population dynamics. Gather up a string of weather data from a convenient weather station and model the time to extinction for a population. Time-to-extinction estimates are making a big splash in the conservation community and they don't require any tedious field validation. Few reviewers will notice that this garbage-in-equals-garbage-out exercise provides no new information on the status of the population. With a hypothetical data set you can model whatever extinction time you want.

If you choose to present data on species assemblages, define your assemblage in a way that maximizes investigator convenience. Unfortunately, rare species are difficult to quantify. A popular gambit is to collect data on a few of the commoner species and consider the result representative of the whole assemblage. If you want to justify habitat disturbance it is generally best to choose early successional species. Area-sensitive forest species should be emphasized by those who want to show that deforestation hurts biodiversity. If this is not convenient, however, one could assume that all species are equally significant; few would notice that global tramp species account for as much biodiversity as do regional endemics. In all probability there is some group of species that can be found to benefit from whatever land-use policy you want to promote.

If you want to go to the effort of quantifying the abundances of all species in an assemblage, simplify your study by basing abundance indices for all species on a single sampling technique. Never mind that there are no techniques that are unbiased among species or among habitats. For example, reptile samplers can rely on an array of pitfall traps and drift fences. Of course, some snake species are rarely caught in pitfall traps, but low estimates of snake abundances do not attract criticism, as it is widely believed that snakes are rare.

If you choose to combine measures of species richness and evenness into a single diversity index, select your index carefully. There are so many measures of diversity that almost any management recommendation can be justified. In some cases, for instance, you may wish to stress how your preferred management prescriptions will improve species evenness in the measured assemblage. If that does not provide the hoped-for answer, you can emphasize within-habitat richness or diversity, using the most supportive of the many available indices. If that still doesn't work, try conflating the concepts of within- and among-habitat diversity. For example, if you want to justify logging of old-growth forest in the face of data showing greater species diversity within old-growth habitats, point out that a combination of old second-growth and recently cleared areas (the combination can be labeled "managed forest") has more species than does old growth alone. It is not hard to pump up species richness measures if you just pool enough habitat types.

Your study (and your management recommendations) will inevitably be linked to your choice of study organism. There is no need to emphasize to readers that diametrically opposed management recommendations might have been obtained by studying a different taxon.

If those strategems don't yield comfortable management recommendations, there are always more creative solutions. For example, congressional revulsion to a U.S. public land agency's practice of converting diverse southern hardwood forests to monotypic pine plantations resulted in passage of a law requiring the agency to maintain the level of diversity that is found in forests regionwide. Given the lack of consensus in the scientific community over the best measure of species diversity, Congress left choice of the applicable diversity index up to the managing agency. The agency chose to measure diversity not in number of tree species but in stand age. Thus, for a rotation age of 50 years, maximal diversity was to be achieved by cutting one tenth of the forest area every five years (reforested as a monoculture). Perfect evenness! Such is the beauty of biodiversity; it can be used to justify creation of a monoculture.

Unfortunately, it is easier to add up the ways in which the concept of biodiversity can be misused than it is to present a simple solution to the extremely complex problem of measuring or maintaining biological diversity. The public is unclear on the concept, and scientists cannot give a simple answer. There is broad agreement only that humankind should prevent anthropogenic extinctions. Perhaps we should build on this consensus rather than undermining it with dubious measurements of biodiversity.

Perhaps we need to recognize that for scientists to combine partial data with advocacy is counterproductive in the long run.

Perhaps conservation biologists need a consensus declaration that short-term, taxonomically narrow, or local diversity studies are inappropriate tools for the long-term conservation of global biodiversity. If anthropogenic declines are our primary concern, perhaps we need to refocus our attention on (1) rangewide status surveys that will provide firm baseline data, (2) evidence that anthropogenic causes are responsible for demonstrable population changes, and (3) identification of the proximate mechanisms that link human activities with species loss. These avenues of study will not be as easy or as much fun as blunderbuss sampling of biodiversity, but they may keep the concept from becoming tawdry through uncritical application.

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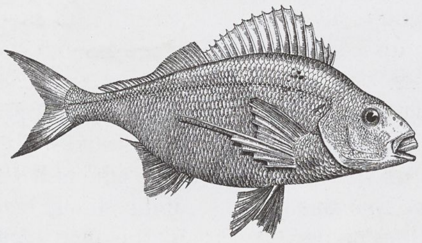

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BIODIVERSITY AND THE CULTURE OF ECOLOGY

The image of the Great Chain of Being epitomizes the moral and religious attention people within the Western tradition have long paid to the diversity of life. From Plato's theory of perfect Forms to the quest of many recent ecologists to find order and balance in nature, philosophers, poets, painters, and scientists have attempted to describe the living world in ways that answer to religious and moral expectations. Ecologists in this century—like theologians and poets in previous centuries—have argued that the diversity of living things results not from mere contingency or chaos but serves larger purposes, instantiates universal principles and ideas, or expresses an intelligible order or a meaningful plan.

In the 11th Century, the French theologian Abelard, following Plato's *Timaeus* (30c), defined one aspect of the Chain-of-Being theme, namely that a sufficient reason explains the existence of every kind of organism. "Whatever is generated is generated by some necessary cause, for nothing comes into being except there be some due cause and reason for it" (cited in Lovejoy 1936). Along with the idea of sufficient reason, the principles of plenitude, continuity, and gradation determined the order of creatures from the least to the greatest in a vast Chain of Being.

These principles have analogies in the ecological theory of recent decades. Plenitude—the principle that the richness and diversity of creation is so great because it expresses the fullness of God's perfection—is found in various versions of the diversity–stability hypotheses, for example, in G. E. Hutchinson's (1959) speculation that there are so many species "at least partly because a complex trophic organization of a community is more stable than a simple one." The themes of gradual continuity and gradation likewise echo in hierarchy theory, the theories of trophic levels, food chains and webs, in the concept of orderly succession, and in other concepts that characterized ecology earlier this century.

Fundamental to the idea of the Great Chain of Being was a belief that God creates nothing in vain. Accordingly, we are obliged to care as

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much for the least creature in nature as for the greatest. The popular analogy associated with Paul Ehrlich that likens species to rivets in the wing of an airplane echoes the well-known passage in Alexander Pope's *Essay on Man*:

> Vast chain of being! which from God began,
> Natures aethereal, human, angel, man,
> Beast, bird, fish, insect, what no eye can
> see . . .
> Where, one step broken, the great scale
> destroyed
> From Nature's chain whatever link you
> strike,
> Tenth, or ten thousandth, breaks the chain
> alike.

Commenting upon the centrality of the Chain of Being metaphor, historian A. O. Lovejoy (1936) observed that according to this tradition, the diversity of nature corresponds to law-like principles that establish its order; the "universe was at least not a many-ringed circus." Lovejoy notes, however, that in the eighteenth century, a controversy arose pitting philosophers like Spinoza and Leibniz, who believed that the principle of sufficient reason necessitated a such a hierarchical order in the variety of nature, against those who followed the British philosopher Samuel Clarke in arguing that only God's essence implied existence, and that contingency pervaded the created world. In 1712, a British poet put that thesis as follows:

> Might not other animals arise
> Of different figure and of diff'rent size?
> In the wide womb of possibility
> Lie many things which ne'er actual may be:
> And more productions of a various kind
> Will cause no contradiction in the mind . . .
> These shifting scenes, these quick rotations
> show
> Things from necessity could never flow,
> But must to mind and choice precarious
> beings owe
> (cited in Lovejoy 1936)

A controversy that rages between those who believe that nature must exhibit a "balance" or "order" and those who argue that it is all chaos and contingency—a many-ringed circus—characterizes ecological debates today as it did cosmological debates in earlier centuries. As we shall see, these two positions—one emphasizing continuity and order in nature, the other emphasizing change—suggest grounds for valuing biodiversity, but they present quite different reasons that biodiversity should be preserved.

The Great Chain of Being Today

Earlier this century, ecologists such as Paul Sears and Frederic Clements, remaining firmly within Great Chain of Being tradition, approached ecology as the study of harmony, continuity, gradation, and equilibrium. Clements, as historian Donald Worster (1977) observes, contended that nature's course "is not an aimless wandering to and fro but a steady flow toward stability that can be exactly plotted by the scientist." Following Clements, Gaian theorists recast the Great Chain of Being in modern terms, representing the earth as a vast superorganism, possessing as much internal order as the organisms that make up its functioning parts.

E. P. Odum (1969), an ecologist who seems among those most indebted to Great Chain of Being analogies, restated the 18th Century principle of plenitude as "the strategy of ecosystem development" which is "directed toward achieving as large and diverse an organic structure as is possible within the limits set by the available energy input and the prevailing conditions of existence." This "strategy" is supposed to lead ecosystems in law-like ways through orderly successive changes to species composition to achieve a state of mature homeostasis in which the stability and diversity of the system are the greatest it can achieve under given conditions. In such a system, just as in the Chain of Being, every possible creature finds its place. In Odum's version of plenitude, this happens, for example, when weedy generalists (*r*-selected species) become replaced by a greater variety of specialized (*K*-selected) plants and animals able to exploit all the niches available to them.

Environmentalists drew many arguments for protecting species from two fundamental ideas: first, that plants and animals, through a hierarchy of relationships, are interconnected and interdependent; and, second, that nature progresses in predictable ways to greater diversity and stability. The hypothesis that the diversity and complexity of ecosystems support their stability, for example, contributed to the enactment of the Endangered Species Act in the United States. The hypothesis first advanced by Odum that salt marshes "outwell" nutrients to feed coastal fisheries served as a powerful argument for preserving those wetlands. The theory of forest succession to a climax state in which biomass remains constant helped people to appreciate the importance of rain forests. One could multiply these examples. The recreation of Great Chain of Being cosmography in post World War II community ecology provided concepts and theories crucial to the efforts environmentalists made to protect biodiversity and to preserve ecological systems.

Yet this traditional way of regarding nature, however helpful as it may be to the goals of environmental protection, cannot in itself suffice to sustain an argument for preserving biodiversity. Just as in the eighteenth century, so today many scholars advance a different approach that emphasizes the historical, the unique, and the contingent in nature. In our effort to appreciate and preserve biodiversity, we must look to this tradition as well—one that eschews theoretical generalizations and attends instead to the careful observation and description of historically contingent objects and events.

The Limits of Community Ecology

The problem with the tradition that runs from Sears and Clements to Odum is not that it fails to capture the concepts of balance, order, harmony, plenitude, and sufficient reason associated with Chain of Being cosmology, for this it does well. The problem is that this school of ecology, by secularizing a traditional vision of nature—by clothing it as science rather than as theology—demystified it. This led to two kinds of difficulties. First, the central theories that linked stability and diversity, that called for an orderly succession of communities, and that arranged creatures in trophic levels and webs opened themselves to empirical and theoretical refutations. In a kind of war between the generations, the students of Odum and of many other founders of community ecology set out to test and in the process debunked theories of forest succession (see Drury and Nisbet 1973, Connell and Slayter 1977), the "stability—diversity" hypothesis (Goodman 1975), the "outwelling hypothesis" (Nixon 1980), and other tenets basic to the discipline.

Second and more relevant to our purposes, biologists who emphasized ecosystem-level properties and processes, such as productivity, energy flow, respiration, trophic webs, nutrient cycling, and efficiency, showed less and less interest in the minute particularities of individual organisms. These ecologists remained committed to a vision of science that insisted on a priori grounds on the centrality of testing by prediction the robustness of abstract and general mathematical theories (Sagoff 1988). According to one historian, community ecologists came to emulate "the language of systems scientists" and began to work on models at the intersection of biology and engineering (Patten 1971).

In the context of these developments in ecology, especially the branch that became known as "systems ecology," both scientists and policy makers found it easier to think of living creatures as resources to be manipulated than as—in John Muir's expression—"conductors of divinity" (Wolfe 1979). To be sure, both community and systems ecology retained faith with the central thesis of the Great Chain of Being that nature exemplifies a timeless and intelligible order rather than sheer historical contingency. By secularizing this religious intuition, however, ecosystem science replaced a priesthood of theologians with one of mathematical modelers and engineers.

It is not surprising that many environmental engineers and other experts found even in ecological theories that took up Great Chain of Being themes grounds not to venerate but to manipulate nature or, as Donald Worster notes, to manage the earth for improved efficiency. "`Governing' of all nature was the dream of these ecosystem technocrats" (Worster 1993, see also Taylor 1988). Experts have used the theory of forest succession, for example, to argue that rain forests, being "climax" or "mature" ecosystems must be in equilibrium and thus cannot add to global oxygen budgets (Whitmore 1980). More generally,

> human beings are more able to use ecosystems at young successional stages, which tend to be more productive. Accordingly, a general characteristic of human development is that we tend to maximize productivity by creating and maintaining ecosystems at such stages (Robinson 1993).

As this passage suggests, ecological science, which many of us pursue because of our love of nature, may fuel a technology intended to manipulate or transform nature. For example, in a well known article, ecologist Dan Janzen views with horror the possibility that agriculturally desirable organisms may be adapted by genetic

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engineering to natural areas, such as rain forests, that remain intact only because they cannot now be efficiently farmed (Allen 1987).

The prospect that genetic engineering may turn rain forests to agricultural use, which dismays Janzen, appeals to others as a professional challenge. Frank Forcella (1984), writing in the ESA *Bulletin*, called upon his colleagues to embrace the "biotechnologist" credo "to engineer and produce plants, animals, and microbes that better suit the presumed needs and aspirations of the human population." He continued:

> Ecologists are the people most fit to develop the conceptual directions of biotechnology. We are the ones who should have the best idea as to what successful plants and animals should look like and how they should behave... Armed with such expertise, are we going to continue investing nearly all our talents in Natural History? . . . Or should we take the forefront in biotechnology, and provide the rationale for choosing species, traits, and processes to be engineered? I suspect this latter approach will be more profitable for the world at large as well as for ourselves.

To summarize: Poets and theologians who described the Great Chain of Being understood the principles of sufficient reason, plenitude, continuity, and gradation in terms of religious beliefs and moral values. Ecological concepts developed earlier this century and in popular vogue today adhere closely to these same principles—optimization is the current version of sufficient reason; diversity of plenitude; succession of continuity; and hierarchy of gradation. Yet, when these concepts occur in scientific theories, they may be shorn of their religious and moral significance. They may then be open to empirical and theoretical refutation. They may also support arguments that back efforts not necessarily to protect nature for its own sake but to manipulate it to meet our consumer demands.

At that point, we may wonder how much we wish the ecological and biological sciences—including genetic engineering—to succeed. Knowledge is power—but it can be the power to control or the power to protect—the power to bend nature to our purposes or to appreciate nature for its own ends.

The Study of Minute Particulars

We have noted that during the eighteenth century, a group of philosophers argued against Great Chain of Being principles to assert the contingency of creation; they harkened back to Aristotle's view that "it is possible for that which has a potency not to realize it" (*Metaphysics* XI 1071b 13). These writers held that the proper appreciation or reflection upon creation does not lose itself in grand theory—the quest for general mathematical laws and principles—but finds enough to admire and appreciate in nature's tiniest details. This approach sees "the world in a grain of sand/ And a heaven in a wild flower," as William Blake wrote in "Auguries of Innocence." It builds knowledge up from the study of minute particulars rather than seeking to deduce it from timeless a priori truths.

Ecologists who supported this approach early this century included taxonomists such as Henry Gleason, who opposed the a priori attribution of balance, equilibrium, succession, and other "systems" properties to nature. He argued that nature is more like a Heraclitean flux than like a Chain of Being. In "The Individualistic Concept of the Plant Association," Gleason (1926) wrote that each species of plant "is a law unto itself."

During the almost 70 years since Gleason wrote, ecologists have emphasized the search for universal theories, mathematical principles, and general properties over the historical study of individual organisms. This may be the reason that ecosystem modelers and theory-builders vastly outnumber trained taxonomists today. Nevertheless, some ecologists are now turning away from system-level analogies with engineering and other mathematical sciences toward "rich descriptions" of individual organisms in their habitats (Slobodkin et al. 1980).

"Whenever we seek to find consistency" in nature, an ecologist has recently written, "we discover change" (Botkin 1990)—thus echoing Gleason's remark that each species is a law unto itself. This biologist compares nature not to a three-ring circus, but to several musical compositions played in the same hall at once, each intruding on the pace and rhythms of the others. Appreciation then comes down to the intense and patient observation of details, not speculation about overarching harmonies. This kind of patient observation and rich or "thick" interpretative description characterizes the study of natural history in contrast to theoretical ecology.

The empirical work of natural history, including taxonomy, has been ignored, even ridiculed, paleontologist S. J. Gould has written, because it does not indulge in the high-priori mathematical modeling thought to characterize "hard" science. Yet our knowledge of species depends entirely on "the historical sciences, treating immensely complex and non-repeatable events (and therefore eschewing prediction while seeking explanation for what has happened) and using the methods of observation and comparison" (Gould 1984).

The essence of historical explanation, Gould (1989) writes, is contingency: A historical explanation does not rest on direct deductions from laws of nature, but on an unpredictable sequence of antecedent states, where any major change in any step of the sequence would have altered the final result. This final result is therefore dependent, or contingent, upon everything that came before—the unerasable and determining signature of history.

Gould (1989) observes that historical narratives that explain the minute particulars of plants and animals at specific times and places "are endlessly fascinating in themselves, in many ways more intriguing to the human psyche than the inexorable consequences of nature's laws." Biologist E. O. Wilson (1992) elegantly takes up this theme in arguing that every kind of organism, large and small—the flower in the crannied wall—"*is* a miracle," but one that makes sense—is explicable—in the context of a rich historical narrative. "Every kind of organism has reached this moment in time by threading one needle after another, throwing up brilliant artifices to survive and reproduce against nearly impossible odds." To study these artifices—to appreciate the toil each species endures to prevail in the vast labor of evolution—is to be moved to more than scientific understanding. As Darwin understood, this understanding fills our minds with reverence and awe.

The Uses of Diversity

The naturalists who built in the 18th and 19th centuries the great museum collections of species would be surprised at the direction ecological science has taken in our century away from natural history and toward mathematical modeling and general theory-building. These naturalists were rather "wanderers and wonderers" who could be fascinated equally by starfish and stars; they studied the living world for the love of it, not to gain power over it. For these scientists, the infinite variety of nature—as Shakespeare said of Cleopatra—did not cloy the appetite it fed, but where it most satisfied it made most hungry. E. O. Wilson has described this orgy of intellectual satisfaction as *biophilia*, which is a love or affiliation with all of the aspects of the living world.

This attitude toward the living world will not necessarily help us to exploit its resources efficiently; it may not even offer us instrumental or prudential arguments for protecting biodiversity. Naturalists do not necessarily insist, for example, that the moths or mites they study serve as rivets holding Spaceship Earth together; nor need they be concerned with the possible medicinal uses of these species. Rather, simply by describing these organisms and the toil of their coming to be, these naturalists show us how deeply these creatures reward our curiosity and inspire our sense that they have a rightful place upon the earth.

Even if natural historians appeal to ethical and aesthetic rather than to economic and instrumental values, they may nevertheless point to two important uses of biodiversity. First, the particular flora and fauna indigenous to a locality constitute along with details of landscape the fundamental characteristics that identify that place. Thus, insofar as a sense of place is important to human beings—insofar as it is important to people themselves to be native to a place—then it is crucial to maintain an affiliation with its native and indigenous species. Many of us worry that the global reach of markets brings with it a kind of cultural homogeneity—that global unity threatens a kind of global uniformity. Only by resisting the leveling effects of the marketplace can we maintain the integrity of communities—and in this context, ecological and human communities will stand or fall together.

Second, the world's endangered and threatened species include many migratory animals as well as other species whose range is international. The protection of these species—and the seas, forests, and other environments that sustain them—thus becomes an international responsibility. In setting up international institutions and regimes, as well as in entering and implementing arrangements like the Biodiversity Convention, nations learn to work together to maintain what the ancients called *res publica*, which is to say, a public place or thing (in ancient times, typically a monument or town square) which every group honors for its his-

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torical meaning or intrinsic value, not necessarily for its economic utility. Thus the concept of *res publica* is to be distinguished from that of a commons, for people create the former because of a shared sense of moral or cultural community; they police the latter to rationalize their competition over resources they would otherwise waste.

Consider, first, the importance of a sense or spirit of place in decisions local communities make in favor of protecting indigenous plants and animals. The concept of place helps us to understand what we deplore about the human subversion of nature and fear about the destruction of the environment. Many of our moral and aesthetic sentiments about nature are rooted in the sense of loss of places we keep in shared memory and cherish with instinctive and collective loyalty. This sense of loss underlies our concern about the decline of diversity and an attendant loss of security—the security one has when one relies on characteristic aspects of places one knows well.

Thus, a principal reason we set about to protect the habitats of native and indigenous species while caring less about the survival of exotic (including engineered) organisms has to do with our commitment to continuity of places—continuity that requires a sense of community with the past, with each other, and with nature. The preservation of biodiversity is the first step we must take in becoming ourselves native to a place.

What may worry us most in the disappearance of species is the prospect, then, of becoming ourselves strangers to the earth, of never quite settling into it, of losing touch with the places that help constitute the identity of our communities, of therefore being at home nowhere. For the sake of our own identities we must maintain the identities of the places where we live—and this entails maintaining its flora and fauna as well as larger landscapes. The motive for saving ecosystems may most fundamentally lie in our need to feel at home where we live—to attach ourselves to what becomes safe and secure because it retains its aesthetic and cultural characteristics in the midst of change.

In this context, the creation of shared places—*rei publicae*—becomes the most serious work of international relations. The point of this work is to allow groups that may compete over resources, ideology, nationality, and other goals to embrace and act upon values they share. In the Biodiversity Convention, in the Mediterranean Action Plan, in regions that govern the North Sea, the Baltic, and other international waters, in rules regulating trade in endangered species, and in other environmental regimes, we find nations that may be at odds over other issues joining together in a common purpose that is ethical, perhaps religious, at its core. It is this act of making peace not only with the rest of creation but also with each other—learning to put aside differences to act on common commitments—that may be the most important outcome of the preservation of biodiversity.

Conclusion

The American ecologist Robert MacArthur in his book *Geographical Ecology* argued that what is important about diversity is not the history of individual species—the sort of thing that interests naturalists—but the principles and patterns that explain diversity from the point of view of an a-historical mathematical and predictive science. "Hence, we use our naturalist's judgment," MacArthur (1972) wrote, "to pick groups large enough for history to have played a minimal role but small enough so that patterns remain clearer." He wondered: "Will the explanation of these facts degenerate into a tedious set of case histories, or is there some common pattern running through them all?"

We have discussed two ways of thinking about nature. The first is that of MacArthur; community and systems ecologists following him invoked concepts such as complexity, equilibrium, stability, orderly succession, and hierarchy that echo the principles of plenitude, gradation, continuity, and sufficient reason found in Great Chain of Being cosmology. Ultimately, these principles go back to Plato who considered ideal forms to be the appropriate objects of knowledge and believed that actual beings and events at best offer only vague clues or hints about those forms. On the other hand, we described a complementary tradition in ecology, going back to Aristotle, that insist upon what MacArthur calls "tedious case histories." This approach appreciates the individuality and contingency of particular things and claims these as the proper objects of knowledge.

Ecologists this century such as MacArthur sought to identify Platonic or intelligible forms in nature; these ecologists worked in the tradition of Great Chain of Being cosmology. While

they took up concepts that have clear theological origins, however, they demystified them in order to give them scientific legitimacy. These concepts therefore lost their religious connotations—their affiliation with and affection for nature—and became central to an effort to predict phenomena in order better to control nature for our efficient use.

In contrast, natural historians took up techniques of observation, taxonomy, and classification, as well as thick description and historical explanation associated not with religion or cosmology but with empirical science ever since Aristotle. These naturalists, however, turned this task into a nearly religious mission, teaching their readers to appreciate and care about the plants and animals they so lovingly described. Naturalists such as S. J. Gould and E. O. Wilson stand firmly within an Aristotelian tradition of empiricism, yet they turn this tradition into a spiritual quest. This is the reverse of ecologists who followed the path of Platonic rationalism and who transformed, however inadvertently, an essentially religious cosmology into a basis for environmental engineering.

Thus, the recent history of ecology presents a paradoxical face. One group of ecologists—followers of MacArthur—took up essentially religious ideas from Great Chain of Being cosmology but divested these concepts of all their spiritual connotations to convert them to the uses of "hard" predictive and universal science. The other group took up the rather dispassionate concepts of systematics and taxonomy, which had constituted the core of biological science since Aristotle, and have endowed these concepts with an almost religious significance.

Each of these approaches gives us strong reasons to value biodiversity. The first tradition, which seeks to predict natural events on the basis of mathematical patterns and principles, helps us to understand the economic and instrumental role biodiversity plays in sustaining ecosystems. This approach warns us against the extinction of species on prudential grounds—for example, because one never knows when one might have a use for some chemical compound they may contain. And even biotechnologists need the raw material that they may recombine to form new genetic worlds for us to conquer and use.

The second approach, which focuses our moral attention on case histories, teaches us to appreciate the wonder of nature and to attach ourselves culturally and aesthetically to the places nature has given us to live. In this context, we are most loathe to surrender even a single species, even if it could be shown not to be economically or instrumentally useful. To those who make this moral commitment to the rest of Creation, even the gesture of identifying and naming a species is a morally important act. Every parent with a new baby—or every child with a new pet—understands that the process of naming is central to the process of taking possession and assuming responsibility. The prospect of the extinction of millions of species, some of which we have not even named, must fill us with remorse that is moral, not just prudential. We say good-bye to what is not yet ours; we are relinquishing what we have not yet possessed.

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A PARADIGM FOR ENVIRONMENTAL MANAGEMENT DECISION-MAKING

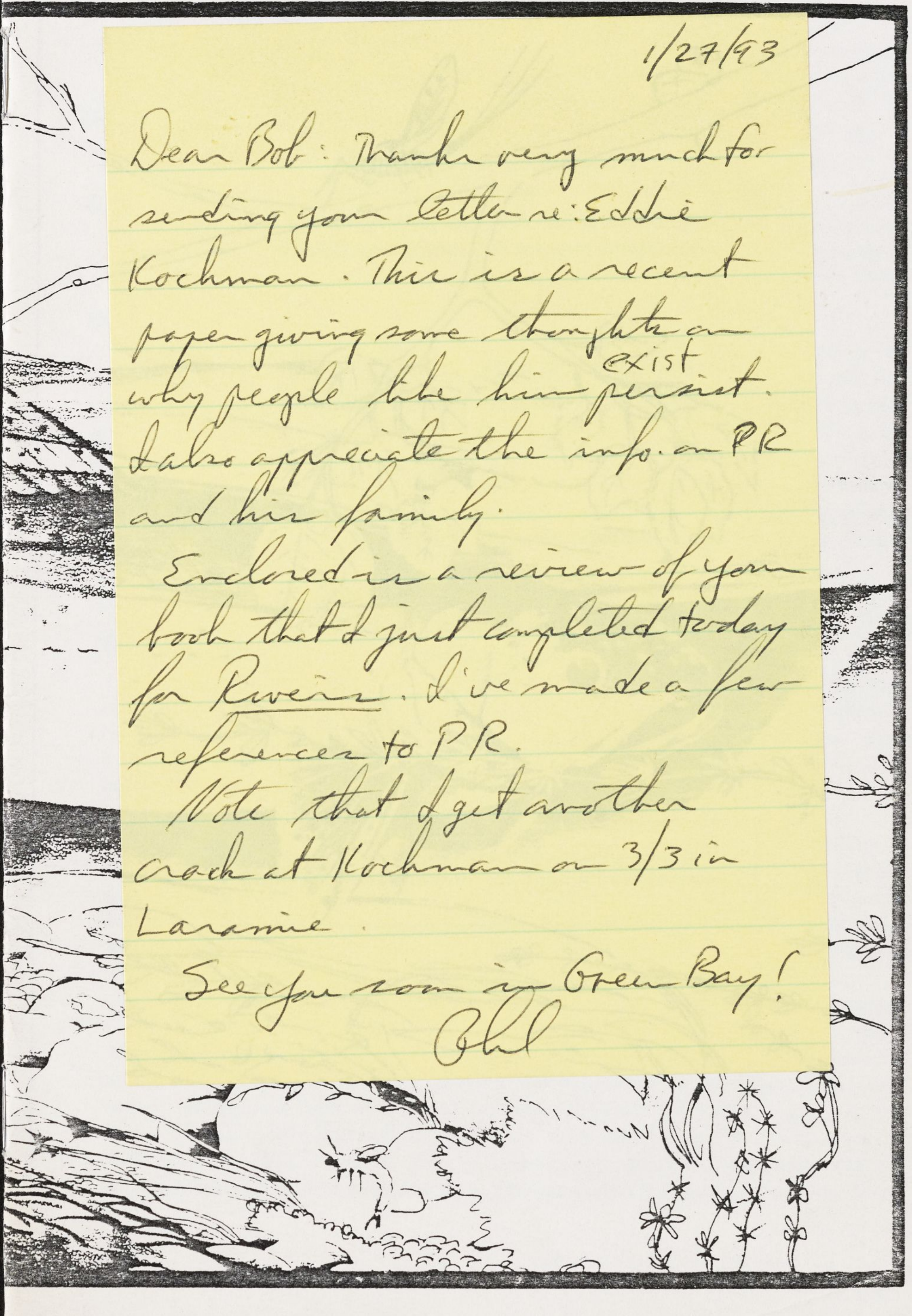
The academic community plays a number of important roles in supporting those of us who are day-to-day practitioners of environmental management. One of these is to provide sound scientific bases for management actions. ESA is to be congratulated for filling this role with the journal *Ecological Applications*. Study of the first volumes shows just how effective this series is at defining the parameters of applied ecology.

Another crucial contribution from academia is ongoing idea generation. To manage the environment in protective, cost-effective fashion, we need innovative, useful ideas for interpreting findings and projecting risks and benefits. Ecology as a whole is just awakening to a key analytical idea: that natural systems in general, and perhaps ecosystems most particularly, operate through "fuzzy," rather than "crisp," processes.

Ecosystems have long been studied as examples of von Bertalanffy-type dynamic control systems (von Bertalanffy 1968). This approach has been heuristically useful (for example, Gist and Crossley 1975, Odum 1986, Elliott et al. 1988), but has proven to be less effective for management. In practice, it is often difficult to reproduce experimental findings at the ecosystem scale. Projected outcomes frequently fail to validate, rendering the uncertainty of management decisions very high, and weakening cost–benefit comparisons.

The problem in linking specific experimental findings to large-scale management may be that von Bertalanffy systems are a limiting case of a more general class of constructs: Zadeh (fuzzy) systems (Zadeh 1965). Fuzzy systems are de-

Biological Diversity in Aquatic Management



1/27/93

Dear Bob: Thanks very much for sending your letter re: Eddie Kochman. This is a recent paper giving some thoughts on why people like him exist persist. I also appreciate the info. on PR and his family.

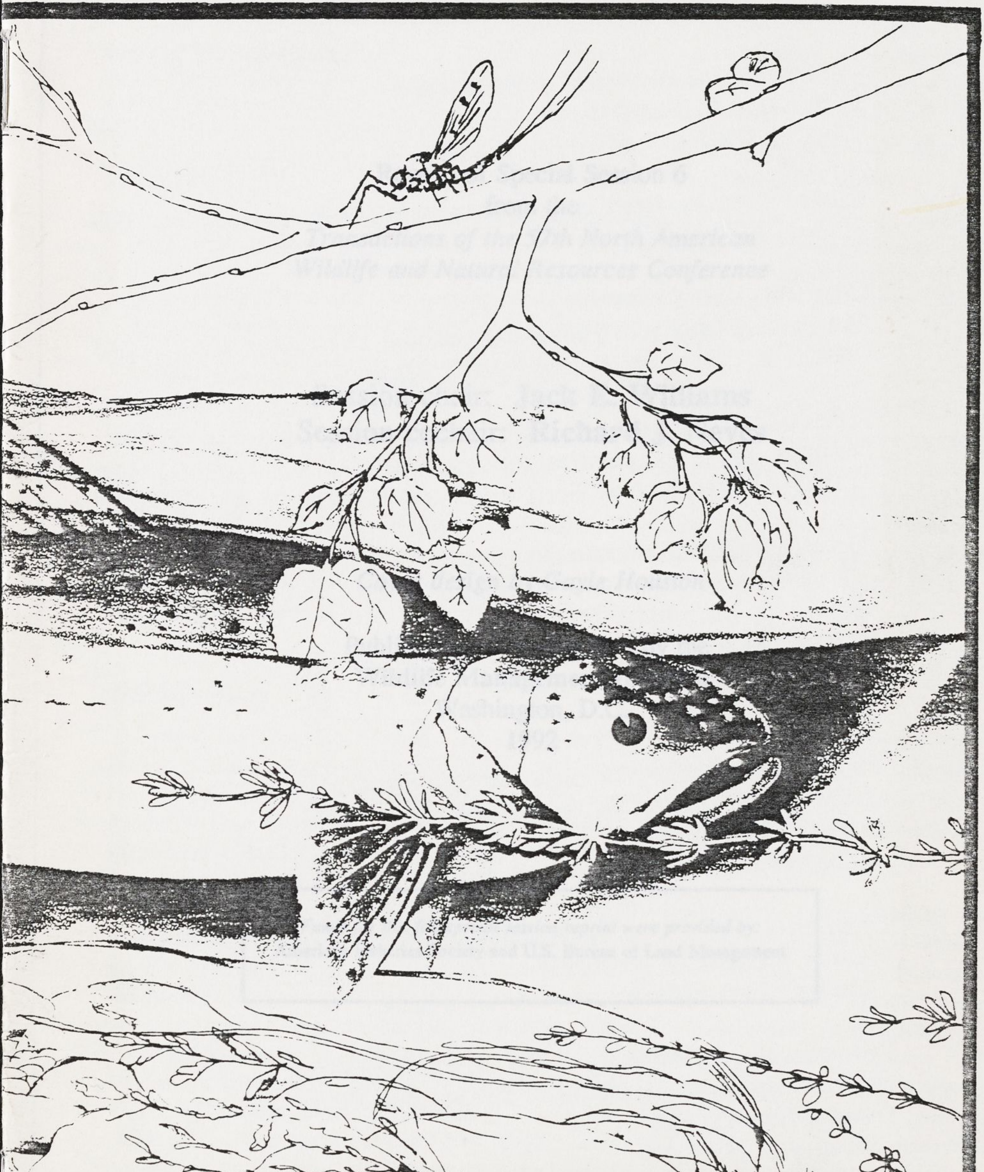
Enclosed is a review of your book that I just completed today for *Rivers*. I've made a few references to PR.

Note that I get another crack at Kochman on 3/3 in Laramie.

See you soon in Green Bay!

Phil

Biological Diversity in Aquatic Management



Biological Diversity in Aquatic Management

Reprint of Special Session 6
from the
Transactions of the 57th North American
Wildlife and Natural Resources Conference

Session chair: **Jack E. Williams**
Session cochair: **Richard J. Neves**

Cover design by Gayle Houston

Published and copyrighted by the
Wildlife Management Institute
Washington, D.C.
1992

Funds for this full special session reprint were provided by:
American Fisheries Society and U.S. Bureau of Land Management

Contents

Ethical Considerations in Conservation of Biodiversity

Edwin Philip Pister
Desert Fishes Council
Bishop, California

Preface

One of the penalties of an ecological education is that one lives alone in a world of wounds. Much of the damage inflicted on land is quite invisible to laymen. An ecologist must either harden his shell and make believe that the consequences of science are none of his business, or he must be the doctor who sees the mark of death in a community that believes itself well and does not want to be told otherwise (Aldo Leopold [*Round River*] 1953).

I write this paper with a measure of idealism, quickened by the harsh reality of continental species endangerment and extinction. I recognize that tradition and established bureaucracy are not easily overcome. Probably nothing is more intransigent than bureaucracy at the policy making level that takes comfort in the status quo. However, we are now experiencing the gentle breezes that inevitably precede the winds of change, and we would be well advised to heed them. As our profession enters into this new era of assuming responsibilities for biodiversity conservation, we should become dynamic and enthusiastic leaders, not petulant dissenters. I hope that what follows will help to clarify this complex matter.

Introduction

During 1992, at the Western Division and National meetings of the American Fisheries Society, sessions addressed an enormously important issue that perplexes our profession, perhaps best defined in the session titles, Western Division: "Endangered Fish Conservation and Sport Fisheries: Managing Resources Between a Rock and a Hard Place;" and National: "Fisheries Goals for the Year 2000: Biodiversity or Benefits?"

A perceptive reader will detect a burgeoning phenomenon first identified by a prophetic Aldo Leopold (1949:221) a half century ago and described in *A Sand County Almanac*: "Conservationists are notorious for their dissensions. . . . In each field one group (A) regards the land as soil, and its function as commodity-production; another group (B) regards the land as a biota, and its function as something broader. How much broader is admittedly in a state of doubt and confusion."

Unfortunately, this dichotomy remains strongly with us today, with the stakes vastly higher in terms of actual and potential loss of biodiversity.

Because of its ramifications, it behooves us to examine the underlying causes of an intriguing mixture of biology, politics and philosophy in an effort to improve overall management direction. The dichotomy is complicated (especially within the states) by budgetary constraints and practices which give lip service to conservation of biodiversity while available financial resources are directed toward conventional management goals. Most state nongame programs are left to survive on "soft" and highly unpredictable funding sources, such as tax checkoff revenues (Williams 1986). Having undergone a Group A to Group B conversion about 30 years ago, and about 10 years into my career (Pister 1985, 1987, 1991a), and having spent countless hours pondering this phenomenon, I offer the following observations.

Discussion

In general, we find four distinct groups expressing professional concern over the conservation and integrity of natural biodiversity:

1. University faculty and students who possess a deep appreciation of the ecosystem and recognize the research potential within a biota, and whose professional existence is strongly related to its integrity. Unfortunately, this group seldom takes an active role in biodiversity conservation, assuming that it will be adequately handled under the stewardship mandate of government agencies. Exceptions to this are the more pragmatic university representatives within (and leading) the Society for Conservation Biology, Desert Fishes Council and similar organizations. University researchers are strong supporters of Leopold's Group B.
2. Biologists affiliated with the private sector: The Nature Conservancy, World Resources Institute, Defenders of Wildlife, National Audubon Society, National Wildlife Federation, Environmental Defense Fund, Wildlife Management Institute, etc., and private consulting firms. Established conservation organizations will be strongly supportive of biodiversity concepts (Group B), whereas private consulting firm personnel will largely reflect the business climate in which they operate. A consultant's projects may be as diverse as an aquaculture proposal suggesting importation of a potentially harmful exotic, or a study involving collection and evaluation of data concerning a critically endangered species. Normally, the consultant will not be an advocate, but will simply do a job or supply information to fulfill an obligation to a client.
3. Federal biologists from resource-related agencies: Fish and Wildlife Service, National Park Service, Bureau of Land Management, Environmental Protection Agency, Forest Service, Bureau of Reclamation, Soil Conservation Service, Corps of Engineers, etc. Because management authority for fish and wildlife populations in public waters is normally relegated to the states, federal biologists generally do not become involved in specific management activities, except through cooperative efforts with state agencies. Activity and attitudes relative to biodiversity conservation are determined primarily by basic agency orientation. For instance, a biologist representing the Office of Endangered Species will be disturbed by a Soil Conservation Service proposal to introduce *Tilapia* into a farm pond located within a drainage containing native fishes, or a Corps of Engineers plan to dam a river critical to the existence of a threatened native plant or rare hydrobiid snail.
4. State fish and wildlife agency biologists. Probably the best example of Leopold's A/B dichotomy is found within this group entrusted with the management of most public waters, although it prevails within other agencies as well. Here, we often find a deep philosophical chasm separating biologists sitting at adjoining desks, and with supposedly similar educational and cultural backgrounds. Why, then, does the A/B dichotomy persist?

Kochman

Possible Causes

It has been my observation that two basic types of biologist are hired by fish and wildlife agencies. First, there are those who develop an early love for fishing and/or hunting and pursue a related career by entering into a fish or wildlife curriculum at a college or university. Major specialty course requirements are supplemented with offerings designed primarily to sharpen technical skills. Foundation courses in the humanities are avoided or minimized, and the student emerges at the bachelor's level better described as trained than educated in the classic sense (Baer 1978, Brown 1987). Such employees have a tendency to remain in Group A throughout their careers. They are technologically competent and, by reflecting agency policy (often with a strong Group A bias), may rise quickly to administrative and policy making levels.

By contrast, there exists another type of student whose broad interest in the life sciences causes him/her to major in biology, zoology, environmental science or some related discipline, often within a Letters and Science curriculum that requires strong grounding in the humanities. During the undergraduate years (usually within the upper division or even in graduate school), the student develops a deep academic interest in fish and/or wildlife and finds that the best way to pursue this interest as a career is within a fish and wildlife agency. In many instances, such a person will gain little or no interest in hunting, fishing or consumptive use of any type. He/she often will be viewed as something of an "oddball" by the Old Guard, which finds it difficult to accept the fact that their obligation (moral, if not legal) is to the entire biological resource and not only to a particular political constituency. Almost without exception, this person will identify strongly with Group B and, when looking at his/her co-worker at the next desk, will find that the communication gap is primarily the result of a very different set of values (Baer 1978). The Group A employee will normally devote his/her career primarily to promoting traditional interests in the Department of Fish and Wildlife, whereas the Group B employee's primary concern will be over the fish and wildlife resource per se. There can be a major difference between the two (Williams 1986).

Changing Times

In the March-April 1979 issue of the American Fisheries Society journal *Fisheries*, five administrators representing different perspectives on fisheries education stated their views concerning curriculum structure. It was their consensus 13 years ago that the profession would be well served by a broadening of curricula to include more humanities courses, and that the concept of pursuing a fisheries speciality only at the graduate level should be given serious consideration, as suggested a decade later in the same journal by Oglesby and Krueger (1989). This was before such awesome environmental issues as global warming, acid rain or tropical rainforest destruction had become household terms. Conservation biology as a formal discipline did not yet exist, nor did its corollary term, biodiversity. To emphasize how the world environment has changed, the March-April 1979 issue of *Fisheries* displayed a snail darter (*Percina tanasi*) and the Little Tennessee River on its cover. That was a very different, and very naive, era.

The past decade has underscored the wisdom of the authors. As we conclude the 1990s, then enter very quickly into the next century, we may be certain that the problems presented to us will become increasingly complex and serious, and that each year, as society and technology evolve, the issues requiring considered judgment from fisheries scientists will become increasingly difficult to solve. They will, in all probability, comprise things that we are unable to comprehend or define at this time. It therefore becomes a matter of urgency that our universities not produce graduates whose skills become obsolete almost before they receive their baccalaureates. A broadly based and relatively unspecialized education emphasizing biological principles can accomplish this and, in the process, help to assure that we do not produce what can quickly become outmoded missiles without guidance systems.

During my undergraduate years at Berkeley, following World War II, before the fish and wildlife speciality in higher education became so widespread, I found it perplexing that, as a wildlife conservation student, I could locate in the course list but two offerings in the field of wildlife, and one (Ichthyology) related to fisheries. When I complained to my adviser, A. Starker Leopold, his response was simple and direct: "We intend to educate you here. You can pick up job skills later." I have since learned that it is much simpler to train an educated person than *vice versa*.

Despite the fact that during my entire six years up through the master's degree I studied only Ichthyology (scarcely a fisheries management course) and two wildlife courses, I somehow survived a 38-year career as a fishery biologist charged with conserving the ecological integrity (and managing sport fisheries where appropriate) within about a thousand waters in the eastern Sierra-Desert regions of California. This area currently supports more recreational use than Yellowstone, Grand Canyon and Glacier national parks combined (Federal Energy Regulatory Commission 1986). Doing so involved contending with a diversity of problems totally unknown to me when I began my career, following graduate school in 1952. My direction was provided by a broad grounding in the humanities and ecological principles, and a value structure based on the philosophies of Starker and Aldo Leopold (Pister 1987). Whereas genetic diversity allows a species the best chance of adapting to new and unexpected conditions, in like manner, a broad and less specialized education in the management of natural resources will best prepare our biologists to handle new and unexpected problems.

What Does the Future Portend?

At a 1991 fisheries leadership workshop sponsored by the American Fisheries Society at Snowbird, Utah, Frank Popper, of the Urban Studies Department of Rutgers University, presented a keynote address entitled: "The Return of the American Frontier: Some Implications for Fisheries," which predicted that, during the twenty-first century, large quantities of privately owned or controlled land in the rural West will be abandoned and revert to public or quasi-public holdings. This will result in enlargement and improved buffering of national parks and forests, their state counterparts, and other public lands. He envisioned major growth in businesses devoted to ecological restoration of land damaged by previous extractive uses, as well as a burgeoning ecological tourism industry. All this underscores the observation that society is moving away from its emphasis on consumptive use toward a different component of the biota. We are returning to a frontier that, in Dr. Popper's words (Popper 1991:A–4): "will offer a magnificent, once-in-history opportunity to create (or recreate) extraordinary habitat, for fisheries and for other habitat uses as well. The combined rise of preservation, decline of a great deal of extraction, and emptyingout of much of the Pacific side of North America will present a remarkable chance to undo our past mistakes and neglect. It is not, perhaps, a chance we deserve, but it is no more than a chance—we also have to be willing to act to take advantage of it. If we succeed, the results will be environmentally and economically spectacular, the world's first sustainable-development frontier. If we are not so fortunate, the results will be disastrous, the historically familiar creation of yet another human-induced wasteland.''

Signs of this shift are already appearing in the bellwether state of California, which, in 1989, sold 29 percent fewer angling licenses than in 1980, although the state's population increased by more than 7 million during that decade. In 1980, about one in 10 Californians bought a fishing license, for a total of 2.3 million. In 1989, about 1.6 million fishing licenses were sold, or one for every 20 Californians. This concept is clearly illustrated by Figure 1, which presents hypothetical supply and demand curves for fish and wildlife resources as we move into the next century, and underscores the need to conserve biodiversity. Components of the total biota,

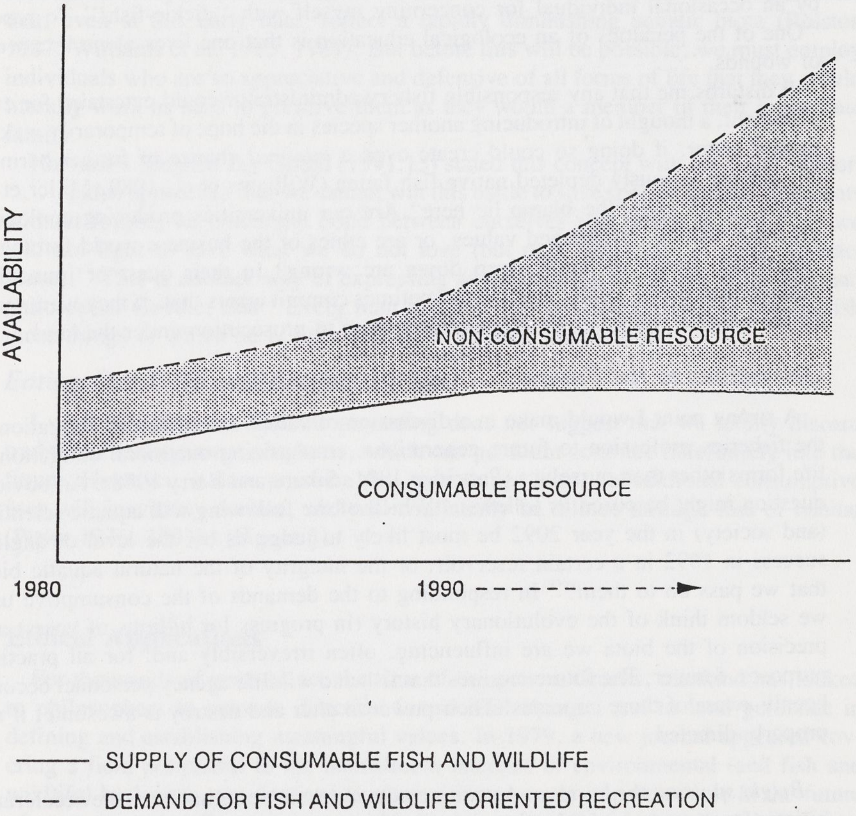


Figure 1. Probable supply and demand trends of North American fish and wildlife resources (adapted from Pister 1991b).

existing in secure habitats, will then essentially comprise a dictionary from which we may write prescriptions for whatever an unquestionably more sophisticated and perceptive society may require (Pister 1976, 1991a, 1991b).

Values and Aquatic Organisms

My fishery values were cemented during a very dramatic afternoon on August 19, 1969, when a graduate student working with me came breathlessly into the office and stated with obvious trepidation that unless we came immediately to the rescue of the only remaining population of the Owens pupfish (*Cyprinodon radiosus*), which was hanging on precariously in a rapidly desiccating, room-sized refugium pond located about eight miles away, we would have an extinct species on our hands (Miller and Pister 1971). In order to do so, however, I would need to cancel a long-planned and highly touted creel census program scheduled for a major reservoir. It was while I was walking back to our pickup truck over rough ground in total darkness later that night, holding the entire world population of an endangered species in two buckets, one in either hand, that the relative values involved really hit me. I wish that everyone working in fisheries science could share a similar experience. It would do much to place our values where they ought to be! Even so, I am still chastised by an occasional individual for concerning myself with "dickie-fish!" To repeat: "One of the penalties of an ecological education is that one lives alone in a world of wounds."

It disturbs me that any responsible fishery administrator could entertain, for even a moment, a thought of introducing another species in the hope of temporarily making fishing better, if doing so could create even a *minimal* chance of further harming our already seriously depleted native fish fauna (Williams et al. 1989, Miller et al. 1989). Where does the blame lie here? Are our universities producing ecological illiterates without established values, or are ethics of the business world forcing us into doing things we know deep down are wrong? In their quest of immediate management goals, public agencies sometimes commit errors that, if they were made by the general public, could even subject them to prosecution under the law!

Obligations to the Future

A strong point I would make in a discussion of values would be the obligation of the fisheries profession to future generations, emphasizing our moral obligation to life forms other than ourselves (Partridge 1981, Sikora and Barry 1978). An obvious question might be posed as follows: "Which of the following will aquatic scientists (and society) in the year 2092 be most likely to judge us by: the level of angling success in 1992 in a certain reservoir, or the integrity of the natural aquatic biota that we pass on to them?" In responding to the demands of the consumptive user we seldom think of the evolutionary history (in progress for billions of years) and precision of the biota we are influencing, often irreversibly and, for all practical purposes, forever. The future requires that fish and wildlife agency personnel become keenly aware of these concepts. Their power to alter and destroy is awesome, if not properly directed.

Bright spots on the horizon. A positive note in recent years has been the accelerated hiring of women as biologists by resource management agencies. It is my impression that women tend to be more sensitive to the mechanisms of the natural world and, as a rule, are far more perceptive than men. It will constitute a major step in the right direction for conservation biology when more women move into administrative positions within their organizations. It has been my observation that women are more likely than men to honor the term "biologist," which presumes understanding and respect for all the complexities and wonder inherent within the ecosystem (Ehrenfeld 1976, 1978, Rolston 1987). As in many parts of society, the fish and wildlife profession has suffered far too long under the almost exclusive domination of males!

Where Do We Go From Here?

Up to this point I have discussed the pragmatic aspects and problems relating to the accomplishment of biodiversity conservation. We need now to direct our efforts toward establishment of a professional ethic that gives it top priority in the planning and budgeting process. To accomplish this, we must hire a generation of fish and wildlife biologists who, with their supervisors, share a deep appreciation of the entire biota and of the evolutionary and ecological relationships that exist within the ecosystem. Gradually then, through an improved funding system for fish and wildlife management agencies and a totally committed and adequate staff to handle this new concept of ecosystem management, we may be able to reverse the downward trends that, even at this early date, reflect a rapidly diminishing aquatic biota (Rolston 1987, Williams et al. 1985, 1989). But before this will be possible, we must employ individuals who are so appreciative and defensive of all forms of life that they would literally work as hard to preserve them as they would a member of their immediate family.

Harvard's Stephen Jay Gould (1991:13) stated this concept with his usual candor: ". . . I also appreciate that we cannot win this battle to save species and environments without forging an emotional bond between ourselves and nature as well—for we will not fight to save what we do not love (but only appreciate in some abstract sense)." This is another way of expressing an observation attributed to the German philosopher Goethe, that "Every man is given only enough strength to accomplish those things of which he is fully convinced of their importance."

Eating Our Cake and Having It, Too!

I wish to emphasize that the preceding does not suggest that we totally discard traditional management programs, which can no doubt continue indefinitely into the future. However, it does presume that, percentage wise, conventional consumptive uses will inevitably decline, and will continually be diluted through loss of habitat (Pister 1976, 1991b) (Figure 1).

Ethical Applications

For thousands of years, since the time of the ancient Greeks, mankind has looked to philosophers to provide direction for societal change, and to lend guidance in defining and establishing meaningful values. In 1979, a new journal appeared covering a field peripheral to the mainstream interests of environmental (and fish and wildlife) biologists, yet destined to play an increasingly important role in the future of an environmentally conscious world. *Environmental Ethics*, described on its cover as "An interdisciplinary journal devoted to the philosophical aspects of environmental problems," brings together writings of philosophers and biologists who detect a strong need for the application of ethical considerations to the causes in which biologists have been engaged for decades, frequently without giving the subject of ethics more than a passing thought. This new emphasis on environmental ethics likely will become one of the most important concepts shaping our destiny as we move into the next century. It will pervade both agency and academe with a philosophy emphasizing what we can do for our fish and wildlife resources, rather than what they can do for us. Contemporary environmental philosophers have already made major contributions in this direction (Callicott 1991, Nash 1989, Rolston 1991).

In a very thoughtful essay concerning conservation of biodiversity, and precipitated by the ongoing Mount Graham red squirrel dilemma, Gould (1990) suggested that we execute a compact with out planet invoking the Golden Rule, a principle utilized by virtually all major religions. Because we cannot ever, in the long run, defeat natural law, and nature holds great power over us, it behooves us to execute such a pact at the earliest possible date. A high priority for the conservation of biodiversity within our profession, which should be a leader in such matters, would constitute a major step in this direction.

Picking up on this same theme, Callicott (1991) proposed a Golden Rule or summary moral maxim of the Leopold Land Ethic: "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" (Leopold 1949:224–225). From this ethic he derives the following "commandments:" "1) Thou shalt not extirpate species or render them extinct; 2) Thou shalt exercise great caution in introducing exotic species into local ecosystems; 3) Thou shalt exercise great caution in extracting energy from the soil and releasing it into the biota; 4) Thou shalt exercise great caution in damming and polluting watercourses; 5) Thou shalt be especially solicitous of predatory birds and mammals" (Callicott 1987). Other environmental philosophers show related concerns (*see* Hargrove 1989, Nash 1989, Rolston 1986, 1988). Undeviating adherence to such a set of "commandments" as guidance for a new ethic would place our concern over conservation of biodiversity on a firm foundation. It would get us "off and running."

Conclusion

During a recent assignment at the Leetown, West Virginia training facility of the U.S. Fish and Wildlife Service, I took an extra day and drove to Thomas Jefferson's home and memorial at Monticello. On his tombstone are inscribed the three lifetime achievements that he wished to be remembered by: "Author of the Declaration of American Independence, of the statute of Virginia for religious freedom, and father of the University of Virginia."

It has been said that a politician's main concern is to be reelected, whereas a true statesman devotes his/her efforts to deeper issues of enduring value to future generations. As I read of Jefferson's magnificent accomplishments, I thought of those in past and present elected office who will be remembered for lesser things. The metaphor likewise applies to our stewardship responsibilities, which extend into the eternities.

It is my feeling that if Aldo Leopold were alive today, he would be disturbed by the fact that persons concerned over the well-being of the nation's fish and wildlife resources should be at even minor odds over such a matter as conservation of biodiversity. It is likely that he would reiterate another of his marvellously prophetic statements, made 59 years ago in his classic text: *Game Management* (1933:405): "There is, in short, a fundamental unity of purpose and method between bird-lovers and sportsmen. Their common task of teaching the public how to modify economic activities for conservation purposes is of infinitely greater importance, and difficulty, than their current differences of opinion over details of legislative and administrative policy. Unless and until the common task is accomplished, the detailed manipulation of laws is in the long run irrelevant."

Epilogue

In a pointed, but very gentle book, entitled *The Rediscovery of North America*, Barry Lopez (1990) described how Europeans have ravaged North America for 500 years in their relentless pursuit of wealth. The greed and devastation first manifested by Pizarro and Cortes are today repeated in the form of acid precipitation, destruction of old growth forests and loss of biodiversity. In their quest for gold, the Spaniards never became aware of the much greater wealth they were destroying in terms of human culture and natural values. Now, half a millennium later, we need to rediscover our continent, and to become aware of the enormous wealth that, although jeopardized, still remains. This wealth is not gold or treasure, but consists of infinitely more valuable things.

"Some hold that this task is hopeless, that the desire for power and wealth is too strong. Without denying in any way the dark flaws of human nature, I wish politely to disagree. . . . We can say, yes, this happened, and we are ashamed. We repudiate the greed. We recognize and condemn the evil. And we can see how the harm has been perpetrated. But, five hundred years later, we intend to mean something else to the world. . . . We must turn to each other and sense that this is possible" Lopez (1990).

The dominoes are showing signs of falling, and we must take heed. There could be no finer way to enter into the next millennium than for the North American conservation community to recognize that basing its programs on an ethically sound foundation will inevitably result in the application of sound biological principle and practice.

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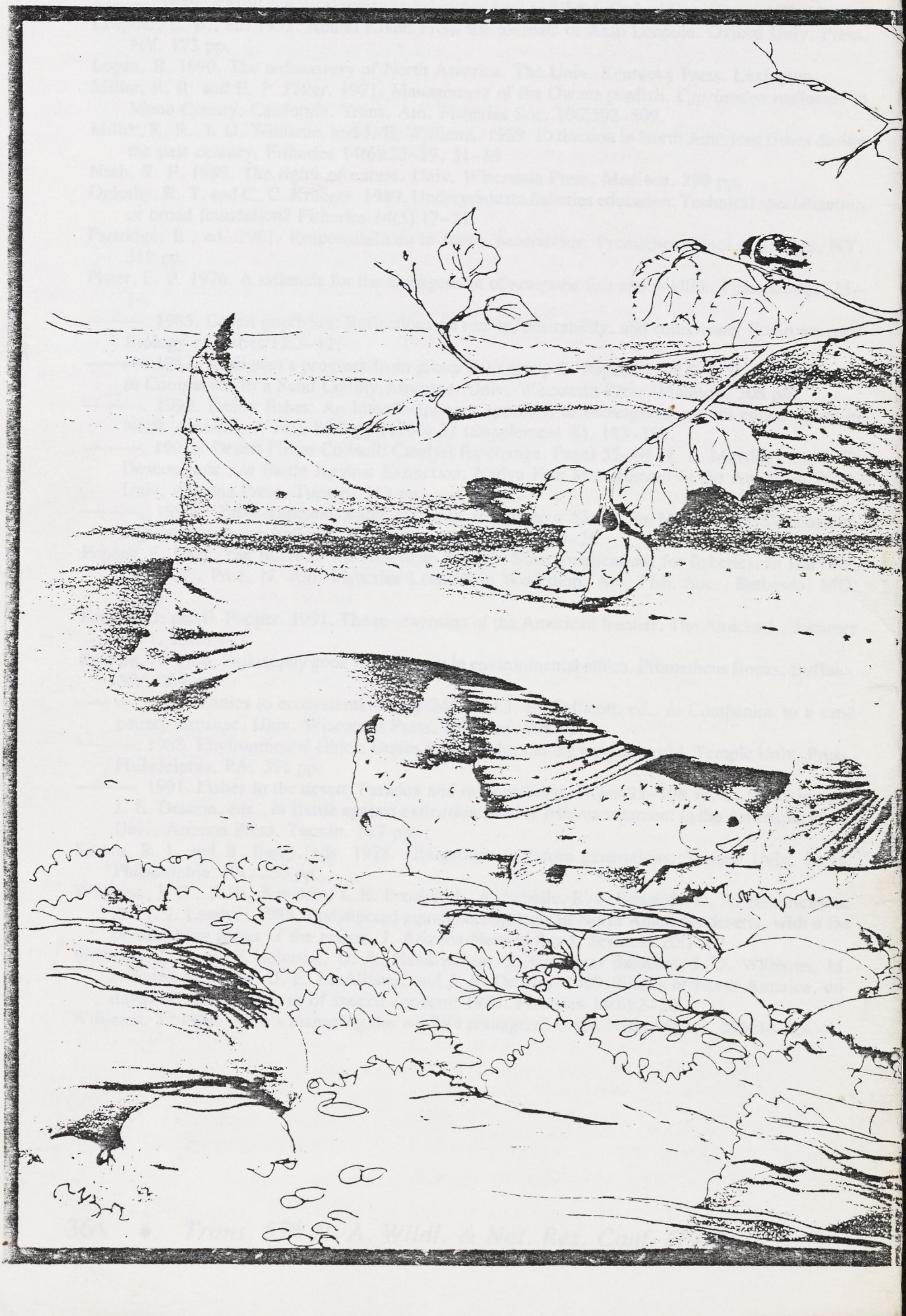

Journal of Fish Biology (1993) **42,** 465–467

Karyotypes of three *Garra* species from Ethiopia

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(*Received 9 April 1992, Accepted 2 August 1992*)

Three cyprinid species from Ethiopia, *Garra dembeensis*, *G. makiensis*, and *G. quadrimaculata*, were found to be characterized by the chromosome numbers (2n) of 50 and by the arm numbers of 82, 84, and 88, respectively.

Key words: cyprinid karyology; *Garra*; Ethiopia.

The range of the cyprinid genus *Garra* includes tropical and subtropical highlands of the Old World from Borneo through Central Asia and India to Zaire and Senegal basins (Menon, 1964). There are reports on karyotypes of two Indian and two Chinese species of the genus (Khuda-Bukhsh *et al.*, 1986; Yu *et al.*, 1987), but no information on chromosomes of African *Garra* species have been published. This note describes the karyotypes of *Garra dembeensis* (Ruppell, 1837), *G. makiensis* (Boulenger, 1903), and *G. quadrimaculata* (Ruppell, 1837) from Ethiopia which appears to be the region of highest species diversity of the genus in the limits of Africa.

Specimens were collected from three localities (nos. 2, 4, 5) in the central Ethiopia. Localities are referred under the same numbers as in our previous report on Ethiopian cyprinid karyology (Golubtsov & Krysanov, 1993) where their description was given. Live samples were transferred to the laboratory in Addis-Ababa, where chromosome preparations were made from the thymus following the method of Kligerman & Bloom (1977). Preparations were treated using a MIAMED automatic chromosome analyser.

For *G. dembeensis* [Fig. 1(a)] four, five and two specimens from localities 2, 4 and 5 respectively, were studied (145 metaphases in total). The diploid chromosome number is 50. The karyotype comprises 32 meta- or submetacentric and 18 acrocentric chromosomes. The arm number is 82.

For *G. makiensis* [Fig. 1(b)] four specimens from locality 4 were studied (56 metaphases). The diploid chromosome number is 50. The karyotype comprises 34 meta- or submetacentric and 16 acrocentric chromosomes. The arm number is 84.

For *G. quadrimaculata* [Fig. 1(c)] five and four specimens from localities 2 and 5, respectively, were studied (94 metaphases). The diploid chromosome number is 50. The karyotype comprises 38 meta- or submetacentric and 12 acrocentric chromosomes. The arm number is 88.

No geographic variation within the chromosome sets both in *G. dembeensis* and *G. quadrimaculata* was found. Sex was recorded only for four specimens of the former species (two males and two females were studied). In contrast to *Garra lamta* from India (Khuda-Bukhsh *et al.*, 1986), no sexual dimorphism within karyotypes was noted.

The diploid chromosome number in three *Garra* species from Ethiopia is the same as in all studied Asian species (Khuda-Bukhsh *et al.*, 1986; Yu *et al.*, 1987). The arm numbers in African species lie in the limits (78–90) peculiar to the Asian species (Khuda-Bukhsh & Barat, 1987; Yu *et al.*, 1987). Thus the Asian and African *Garra* species, together with all karyologically studied *Labeo* species (Vasil'ev, 1985; Paugy *et al.*, 1990), represent the evolutionary diploid lineage of the subfamily Cyprininae (*sensu* Howes, 1987) in which most other taxa appear to be evolutionary polyploids.

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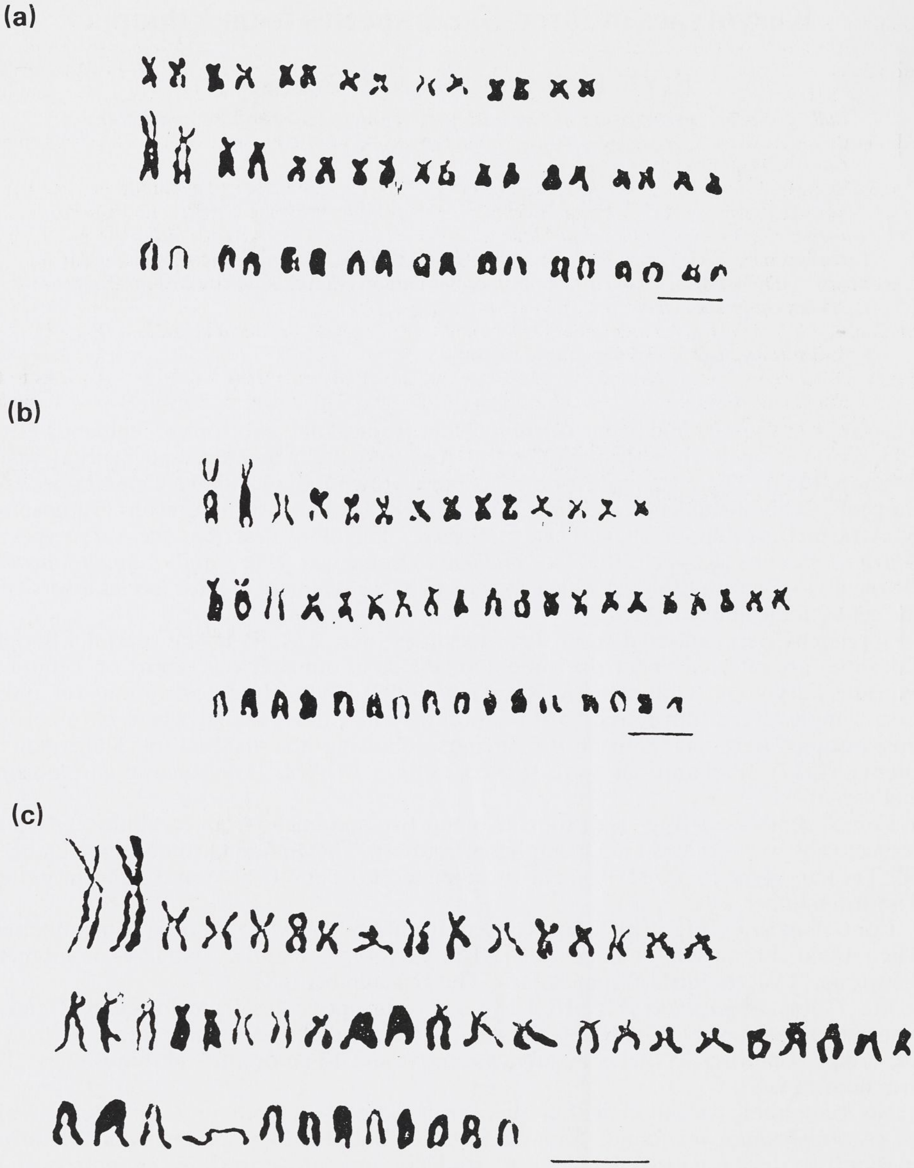

FIG. 1. Karyotypes of (a) *Garra dembeensis*, (b) *G. makiensis*, and (c) *G. quadrimaculata*, taken with a MIAMED video processor. Scale bar, 5 μm.

Journal of Fish Biology (1993) **42,** 445–455

Karyological study of some cyprinid species from Ethiopia. The ploidy differences between large and small *Barbus* of Africa

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(*Received 9 April 1992, Accepted 2 August 1992*)

Chromosome sets of nine species of *Barbus* and a species of *Varicorhinus* from Ethiopia were investigated. All large *Barbus* (*B. bynni*, *B. intermedius*, *B. ethiopicus*) and *V. beso* are shown to have 2N = 150, whereas all small *Barbus* (*B. anema*, *B. kerstenii*, *B. paludinosus*, and three unidentified (probably undescribed) species have 2N = 50. Based on the karyological data and on the published morphological data, an independent origin of small and large *Barbus* of Africa is suggested. The authors believe that large *Barbus* of Africa constitute a monophyletic group and that this group has no sister-group relationships with any of the small *Barbus* of Africa.

Key words: karyology; ploidy differences; *Barbus* phylogeny; Ethiopia.

I. INTRODUCTION

In spite of the high species diversity of the African cyprinids, data on their chromosomes are scarce. At the same time, complicated taxonomic situations scattered in this group need the use of various approaches including karyology. This is the case for the genus *Barbus* which in Africa contains about 300 species (Lévêque & Daget, 1984).

From the taxonomic point of view, the genus *Barbus sensu lato* was called ‘ a monstrous aggregation ’ (Myers, 1960, p. 213) and this is still true. With or without appropriate reasons the Indian, Chinese and Indo-Australian species of the genus are placed by most modern authors into the Asian genera *Puntius, Tor, Acrossocheilus* etc. The remaining species belong to three groups, *Barbus sensu stricto*, whose range includes Europe, the Mediterranean region and the Middle East, some Central Asian forms and the large stock of the African species (Howes, 1987).

In accordance with morphological characteristics the African species in their turn are divided into two groups—the so called small *Barbus* and large *Barbus* of Africa (Boulenger, 1911; Banister, 1987). The small *Barbus* are characterized ‘ by a relatively small adult size (mostly much less than 200 mm S.L.) and by the presence of radiating striae on the scales ’, in contrast with the large *Barbus*, ‘ which generally reach a larger adult size (mostly much greater than 200 mm S.L.) and have parallel or converging striae on the scales ’ (Banister, 1987, p. 115). Until now the phyletic and genetic relationships between these two groups as well as between them and other barbins *sensu* Howes, 1987 have been obscure.

The latest karyological findings seem to promise some progress in this field. Among small *Barbus* from southern Africa N = 24 is reported for *B. viviparus*

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Weber, 1897 (Post, 1965) and 2N = 50 for *B. barilioides* Boulenger, 1914 and *B. holotaenia* Boulenger, 1904 (Rab, 1981). Recently Oellerman & Skelton (1990) revealed a high ploidy level (2N = 148–150) in five yellowfish, large *Barbus* species from southern Africa: *B. aeneus* (Burchell, 1822); *B. capensis* Smith, 1841; *B. kimberleyensis* Gilchrist & Thompson, 1911; *B. natalensis* Castelnau, 1861 and *B. polylepis* Boulenger, 1907. These authors also recorded (by referring to Oellerman's unpublished thesis) the same ploidy level in additional large *Barbus* species, *B. marequensis* Smith, 1841, and in *Varicorhinus nelspruitensis* Gilchrist & Thompson, 1911.

Oellerman & Skelton (1990) did not discuss the karyological differences between the large and small *Barbus* species. They believe that their data support ' a hypothesis of monophyletic origin of the southern African yellowfish and their allies ' (*op. cit.*, p. 113). So they suggest that in the limits of Africa, high ploidy levels are peculiar to several cyprinid species from southern Africa. The other possibility involves the occurrence of high ploidy levels in the large *Barbus* species group as a whole as well as in all African species of the genus *Varicorhinus*. In this case the differences in ploidy level between small African *Barbus* species and large *Barbus* and *Varicorhinus* species should be observed in different regions of Africa. Up until now there has been no information on karyotypes of African *Barbus* species other than for those from southern Africa.

The purpose of this paper is threefold: (a) to estimate the ploidy level in the Ethiopian representatives of the large *Barbus* species group and in the Ethiopian species of the genus *Varicorhinus*; (b) to study the karyotypes of small *Barbus* from Ethiopia, and (c) to account for the karyological peculiarities of these groups in terms of phylogeny.

II. MATERIALS AND METHODS

Specimens were collected from 12 localities in central and south-western Ethiopia (Table I) using gillnets, cast nets, frame nets, and electrofishing. Locality 1 is in the White Nile basin, localities 2 and 3 in the Blue Nile basin and the others are several enclosed drainage systems of the Ethiopian Rift Valley (4 and 5 the Awash R. basin; 6 and 7 the Ziway-Langeno Lakes basin; 8 to 10 the Abaya Lake basin and 11 and 12 the Chamo Lake basin). Field work was carried out in the framework of the Joint Ethio-Russian Biological Expedition (JERBE) during December–March 1990–1991. Live samples were transferred to the field camps where chromosome preparations were made from the thymus following the method of Kligerman & Bloom (1977). For three specimens of *B. intermedius* Rüppell, 1837 from the Kulfo R. meiotic metaphases were prepared by the same technique using ripe testes. Preparations were treated with the use of an automatic chromosome analyser MIAMED (Germany).

In the course of field sampling we failed to record the sex of some karyologically investigated specimens (Table I), as well as to preserve some of them. But the majority of those studied, and all of those collected at the same time from all investigated populations were preserved and deposited in the Ichthyological Department of the Zoological Museum of Moscow State University under the provisional labels of the JERBE.

The systematics of Ethiopian cyprinids are not well-elaborated, but species identification was based on the works of Boulenger (1911), Greenwood (1962) and Banister (1973, 1987). *B. kerstenii* Peters, 1868 has not been reported previously for Ethiopia. The unidentified *Barbus* species recorded in our study as 1–3 are most likely undescribed taxa. According to their size and scale structure they undoubtedly must be considered as small *Barbus* species. Morphological description of these species will be given elsewhere.

On the Relation of Synecology and Natural History to the Wonder of Life: A Reply to Sagoff

The vocation of practicing ecologists is, for the most part, a labor of love. The struggles and frustrations inherent in a career in ecology probably would not be tolerated if ecologists did not feel strongly about their chosen subject matter. In this regard, I find that I agree wholeheartedly with the general tenor of the sentiments expressed in an engaging article by Mark Sagoff (1993) regarding the need to preserve biodiversity. These sentiments are essentially embodied in the following proposition:

> *For the sake of our own identities we must maintain the identities of the places where we live—and this entails maintaining its flora and fauna as well as larger landscapes. The motive for saving ecosystems may most fundamentally lie in our need to feel at home where we live—to attach ourselves to what becomes safe and secure because it retains its aesthetic and cultural characteristics in the midst of change.* (Sagoff 1993:379)

However, the relationship described by Sagoff (1993) between "the culture of ecology" and non-economic justifications for preserving biodiversity is unnecessarily oversimplified. The article distinguishes two approaches to ecology: (1) the theoretical study of communities and ecosystems (synecology), and (2) the natural history of organisms and species (autecology). The former approach is traced to "clear theological origins" as symbolized by the "Great Chain of Being" metaphor of Lovejoy (1936). However, the subdiscipline of synecology, as epitomized by the works of Robert MacArthur, "demystified" this metaphor in order to confer scientific legitimacy, and in the process synecology was reduced to *technology*. Consequently, synecology is unable to provide a basis for the proper appreciation of the wonder of nature. On the other hand, the "rich descriptions" afforded by natural history, as exemplified by the works of Edward O. Wilson and Stephen Jay Gould, provide such a basis for a proper appreciation of the wonder of nature by focusing our moral attention on case histories. "This approach sees 'the world in a grain of sand/ And a heaven in a wild flower,' as William Blake wrote in 'Auguries of Innocence' " (Sagoff 1993:377).

Scientists (including ecologists) tend to be a hard-nosed lot, among whom the percentage of atheists seems to be fairly high. Nevertheless, the capacity to appreciate the wonder of nature (even among theoretical community and ecosystem ecologists) is at least as widespread. More importantly, it is unclear why the scientific study of the dynamics of communities and ecosystems should destroy any sense of the wonder of nature—or even crush religious feelings. (In Boulder, Colorado, at least one Church of Gaia sponsors weekly drum-beating sessions!)

In this regard, it must be remarked that the portraits of MacArthur, Wilson, and Gould painted by Sagoff distort their true attitudes towards nature. Robert MacArthur was no flinty-eyed biotechnocrat. In Wilson's own words:

> *He was not a mathematician of the first class—very few scientists are . . . —but he joined superior talent in that field with an extraordinary creative drive, decent ambition, and a love of the natural world, birds, and science, in that order.* (Wilson 1984:68)

The collaboration between MacArthur and Wilson that led to the publication of *The Theory of Island Biogeography* (MacArthur and Wilson 1967) was undertaken not "in order better to control nature for our efficient use" (Sagoff 1993:380), but for the sheer love of discovery (Wilson 1984:67-74). Moreover, island biogeography provides the theoretical mainstay of conservation biology not only to preserve potentially useful chemical compounds, but also to preserve the wonder of nature embodied in every single species that Sagoff is so loath to surrender.

Much pleasure can be derived from the pursuit of antiquarian natural history for its own sake, but that is not the whole story. According to Gould (1989:281): "The historical scientist focuses on detailed particulars—one funny thing after another—because *their coordination and comparison* permits us, by consilience of induction, to explain the past . . ." (emphasis added).

Similarly, Wilson (1992:5) describes his personal thoughts before an impending storm over the Amazon:

> *I sorted the memories this way and that in hope of stumbling on some pattern not obedient to abstract theory of textbooks. I would have been happy with* any *pattern. The best of science doesn't consist of mathematical models and experiments, as textbooks make it seem. Those come later. It springs fresh from a more primitive mode of thought, wherein the hunter's mind weaves ideas from old facts and fresh metaphors and the scrambled crazy images of things recently seen.*

Thus we see that theory per se does not capture the wonder of nature. Theory is, however, a reflection—is indeed a product of—the wonder of nature to be found in the patterns that cut across rich descriptions of minute particulars. Consequently, Sagoff's distinction between synecology and natural history in relation to the proper appreciation of the wonder of nature (in the transcendental sense of Emerson and Thoreau, see Norton [1991]) seems arbitrary.

Sir J. Arthur Thomson, late Professor of Natural History at the University of Aberdeen, in an essay entitled "The Wonder of Life," remarked on the sentiment expressed in the phrase "the world in a grain of sand/ And a heaven in a wild flower":

> *We must not, however, exaggerate a truth into a fallacy by pretending that all things are equally impressive. For the intensity of the appeal depends on our personal susceptibility* and on our knowledge of what we are looking at, *as well as on objective qualities. To most of us a diamond is more impressive than a dewdrop, and an eagle than a midge.* (Thomson 1936:311, emphasis added)

So it is with communities and ecosystems. Synecology has not "demystified" nature. Quite the opposite: every advance leads further to the ultimate mystery as described by Thomson (1936:316):

> *We think of the [rich descriptions of natural history]; but the big fact is that the World of Life is shot through and through, and up and down, with a quality which affords the highest product of evolution one of his finest joys, and surely gives him glimpses of some harmony lying deep in the heart of things, especially in those that live. We are wise to recall Emerson's profound saying: "I do not so much wonder at a snowflake, a shell, a summer landscape, or the glory of the stars; but at the necessity of beauty under which the universe lies."*

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[1994]

Proc. Natl. Acad. Sci. USA
Vol. 91, pp. 6764–6771, July 1994
Colloquium Paper

This paper was presented at a colloquium entitled "Tempo and Mode in Evolution" organized by Walter M. Fitch and Francisco J. Ayala, held January 27–29, 1994, by the National Academy of Sciences, in Irvine, CA.

Tempo and mode in the macroevolutionary reconstruction of Darwinism

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ABSTRACT **Among the several central meanings of Darwinism, his version of Lyellian uniformitarianism—the extrapolationist commitment to viewing causes of small-scale, observable change in modern populations as the complete source, by smooth extension through geological time, of all magnitudes and sequences in evolution—has most contributed to the causal hegemony of microevolution and the assumption that paleontology can document the contingent history of life but cannot act as a domain of novel evolutionary theory. G. G. Simpson tried to combat this view of paleontology as theoretically inert in his classic work, *Tempo and Mode in Evolution* (1944), with a brilliant argument that the two subjects of his title fall into a unique paleontological domain and that modes (processes and causes) can be inferred from the quantitative study of tempos (pattern). Nonetheless, Simpson did not cash out his insight to paleontology's theoretical benefit because he followed the strict doctrine of the Modern Synthesis. He studied his domain of *potential* theory and concluded that no *actual* theory could be found—and that a full account of causes could therefore be located in the microevolutionary realm after all. I argue that Simpson was unduly pessimistic and that modernism's belief in reductionistic unification (the conventional view of Western intellectuals from the 1920s to the 1950s) needs to be supplanted by a postmodernist commitment to pluralism and multiple levels of causation. Macro- and microevolution should not be viewed as opposed, but as truly complementary. I describe the two major domains where a helpful macroevolutionary theory may be sought—unsmooth causal boundaries between levels (as illustrated by punctuated equilibrium and mass extinction) and hierarchical expansion of the theory of natural selection to levels both below (gene and cell-line) and above organisms (demes, species, and clades). Problems remain in operationally defining selection at non-organismic levels (emergent traits vs. emergent fitness approaches, for example) and in specifying the nature and basis of levels, but this subject should be the central focus in formulating a more ample and satisfactory general theory of evolution on extended Darwinian principles.**

Darwin's Uniformitarianism and the Downgrading of Macroevolution

We yearn to capture the essence of complexity in a line. Rabbi Hillel (*ca.* 30 B.C.–A.D. 10) wrote: "What is hateful to you do not do to your neighbor. That is the whole Torah. The rest is commentary." And Marcus Aurelius, a century later and a culture apart, stated: "Look to the essence of a thing, whether it be a point of doctrine, of practice, or of interpretation."

But conceptual complexity is not reducible to a formula or epigram (as we taxonomists of life's diversity should know better than most). Too much ink has been wasted in vain attempts to define the essence of Darwin's ideas, or Darwinism itself. Mayr (1) has correctly emphasized that many different, if related, Darwinisms exist, both in the thought of the eponym himself, and in the subsequent history of evolutionary biology—ranging from natural selection, to genealogical connection of all living beings, to gradualism of change.

It would therefore be fatuous to claim that any one legitimate "essence" can be more basic or important than another. Yet I wish to focus on a Darwinism that is more pervasive than some of the other meanings—a status won by its role as the fundamental operational, or methodological postulate of all Darwin's theorizing and experimentation.

Charles Lyell was Darwin's guru and intellectual father figure. Darwin commented, in a statement that (for once in his writing) does not reek of false modesty in proper Victorian taste, "I always feel as if my books came half out of Lyell's brain" (2). Much of Lyell's thinking did not contribute to Darwin's evolutionism and may have acted as an impediment to transmutation—in particular, Lyell's steady-state vision of change without direction. But we can scarcely doubt that Lyell's major working postulate and philosophical premise—his uniformitarian vision—became just as firmly embedded in Darwin's thought and scientific action.

Lyell's uniformitarianism held that the full panoply of past events, even those of greatest extent and apparent effect, must be explained as extrapolations from causes now operating at their current observable rates and intensities. In other words, and invariably, the small and immediate may be extended and smoothly accumulated—drop by drop and grain by grain—through time's immensity to produce all scales of historical events. Time is the great enabler. No uniquenesses should be attributed to events of large scale and long times; no principles need be established for the great and the lengthy; all causality resides in the smallness of the observable present, and all magnitudes may be explained by extrapolation.

Darwin accepted and promulgated Lyell's uniformitarian vision in all its uncompromising intensity. Extrapolationism (the methodological side of uniformity) underlies and unites the otherwise disparate pieces and opinions in the *Origin of Species*. What other principle could coordinate, for example, Darwin's hostility to mass extinction (ref. 3, pp. 317–329), his brilliant section on graded structural transition in the evolution of complex and "perfect" organs like the eye (ref. 3, pp. 186–189), his initial case of pigeon breeding as a model for change at all scales (ref. 3, pp. 20–28), and even his choice of the phrase "natural selection" as an analogy to small-scale changes produced by breeders and called "artificial selection."

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Consider just two statements from the *Origin of Species* on the power of geological time to build small and present changes into any observed or desired effect. First, on nature's greater power based on time and fuller scrutiny:

> As man can produce and certainly has produced a great result by his methodical and unconscious means of selection, what may not nature effect? Man can act only on external and visible characters: nature cares nothing for appearances. . . She can act on every internal organ, on every shade of constitutional difference, on the whole machinery of life. . . How fleeting are the wishes and efforts of man! how short his time! and consequently how poor will his products be, compared with those accumulated by nature during whole geological periods. (ref. 3, p. 83)

Second, on time's promotion of the infinitesimal to great magnitude:

> It may be said that natural selection is daily and hourly scrutinising, throughout the world, every variation, even the slightest; rejecting that which is bad, preserving and adding up all that is good; silently and insensibly working, whenever and wherever opportunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life. We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages. (ref. 3, p. 84)

The pure extrapolationism of Darwin's uniformitarian perspective creates an enormous, if not fatal, problem for paleontology. We would like to be a source of meaningful evolutionary theory, for this discipline explains the patterning of the objects we study. But if every event at our scale may be built by extrapolation from a present that contains all causes, then we have no theoretical contribution to make. We are still needed in a lesser role, of course, for history is massively contingent, as Darwin well knew, and theory must therefore underdetermine actual events. But paleontology, in this status, only provides phenomenology—a descriptive accounting, dedicated to documenting that life followed this particular pathway, rather than another route equally plausible in theory. Moreover, paleontology, in Darwin's view, cannot even provide particularly good phenomenology (however honored *faute de mieux*) because an imperfect fossil record so blots, confuses, and distorts the pathway. Remember that Darwin's first geological chapter bears no triumphant title, but rather the apologetic: "On the Imperfection of the Geological Record."

The demotion imposed by pure extrapolationism—to description devoid of theory—must be the chief source of paleontology's curiously low and almost ironic reputation: to be beloved and glamorized by the public (with a series of images from *Indiana Jones* to *Jurassic Park*), and almost invisible within professional halls of status and funding. Consider two assessments of our absent contribution to evolutionary theory. Sadly, as Julian Huxley notes in beginning the first quote, paleontologists have often defended their own debasement—an all too common phenomenon noted among slaves, hostages, and other oppressed people who adopt the assessments of their captors (psychologists even have a label for it, as the Patty Hearst syndrome). Huxley wrote in the book that gave our theory its name (ref. 4, p. 38):

> As admitted by various paleontologists, a study of the course of evolution cannot be decisive in regard to the method of evolution. All that paleontology can do in this latter field is to assert that, as regards the type of organisms which it studies, the evolutionary methods suggested by the geneticists and evolutionists shall not contradict its data.

And even so iconoclastic a morphologist as D. Dwight Davis stated for the Princeton meeting on genetics, paleontology, and evolution (ref. 5, p. 77)—the gathering that oversaw the foundation of our major professional society and its journal, *Evolution*:

> Paleontology supplies factual data on the actual rates of change in the skeleton and the patterns of phyletic change in the skeleton. Because of the inherent limitations of paleontological data, however, it cannot perceive the factors producing such changes. Attempts to do so merely represent a superimposition of neobiological concepts on paleontological data.

Such invalid statements in professional publications often follow an unfortunate path towards inclusion in basic textbooks—and errors in this particular medium are almost immune to natural selection, as extinction-proof as a living fossil in the deep ocean. One major, and very fine, introductory text (ref. 6, p. 524) states:

> Evolution can be studied on the population level only with living organisms. The fossil record provides too few data to allow such treatment; it merely allows paleontologists to reconstruct the history of animal and plant groups [the restriction of our efforts to descriptive phenomenology]. The population approach makes it possible to ask such questions as: What is the rate of evolution in a given species? What factors influence the course or rate of evolution? What conditions are necessary for evolution to begin or cease?

Funny. I would include these three questions within a set most amenable to resolution by the data of fossils and their temporal distribution!

As a final illustration of the reductionistic biases that still beset this most comprehensive of fields, and of the usual tendency to ignore or devalue theory based on whole organisms or long times, the assigned reporter for *Science* magazine presented a remarkably skewed and parochial view of the conference that honored Simpson's *Tempo and Mode* at its half-century, and formed the basis for this published symposium (7). The meeting itself was broad and comprehensive, with talks spanning a full range of levels and durations, from molecules at moments to faunas over geological periods. Yet the reporter ignored about two-thirds of the presentations, including all from Simpson's own professional domain, and focused entirely upon molecular insights—a central issue to be sure, but surely not the exclusive or even the primary theme of a meeting called to honor Simpson's work and its sequelae. Under the headline "Will Molecular Data Set the Stage for a Synthesis," *Science*'s one-dimensional reviewer got Simpson's title wrong and then stated:

> Fifty years ago, the great evolutionary biologist George Gaylord Simpson . . . published a classic volume called *Tempo and Mode of* (sic) *Evolution*. . . . Fifty years later, 250 leading evolutionary theorists gathered in Irvine, California at a symposium in Simpson's honor. Appropriately, the aim of the symposium was to provide a Simpsonian overview of the field, and the conclusion was that its tempo of change is rapid, and one of the main modes of change is the acquisition of new data from molecular biology. As one presentation after another confirmed, molecular biology is offering researchers a multitude of new genetic clues about evolutionary change.

A picture of Simpson, smiling benignly (as he did only rarely in life), graces the page. But I can guarantee *Science*'s reporter that Simpson's ghost is raging at the exclusion of his own field from the primary account of his splendid party.

Tempo and Mode: A Potential Solution Undermined

The conventional view of the Modern Synthetic theory of evolution (often called or equated with Neo-Darwinism) envisages two sequential stages of development: formulation of the population-genetic core in the 1920s and 1930s through the work of R. A. Fisher, Sewall Wright, and J. B. S. Haldane; and alignment of more traditional disciplines in natural history with this central theory in a series of books beginning with Dobzhansky in 1937 (8), and continuing with Mayr in 1942 for systematics (9), Simpson in 1944 for paleontology (10), and Stebbins in 1950 for botany (11), among several others. Simpson's *Tempo and Mode in Evolution*,* published 50 years ago, is our century's most important book in paleontological theory, and my profession's chief contribution to the evolutionary sciences.

Simpson wrote *Tempo and Mode* to assert a distinctive theoretical corner for paleontology in evolutionary discussion and to counteract the denigration discussed in the first section of this paper. (That he was not entirely successful will be evident from the fact that most of the deprecatory quotations, cited earlier in this article, postdate the publication of his book. I shall argue, in this section, that Simpson failed because he bowed to the wrong solution in claiming that he could locate nothing distinctive after correctly defining a domain where one might look.) He spoke for paleontology, and against the extrapolationist vision, with some bravado in his introduction (ref. 10, p. xvii):

pop; vs, evol. genetics!

> They [geneticists] may reveal what happens to a hundred rats in the course of ten years under fixed and simple conditions, but not what happened to a billion rats in the course of ten million years under the fluctuating conditions of earth history. Obviously, the latter problem is much more important.

Tempo and Mode, like so many seminal books, lies completely outside the traditions of its profession. To be sure, paleontologists had written copiously about "evolution;" but, in the profession, this word referred to the documentation of history, specifically to the establishment of phylogeny, not to a study of processes and mechanisms. Paleontological works on evolution proceeded in descriptive and chronological order. If they attempted any closing statements on theoretical generalities, they tried to portray such conclusions as inductions in the enumerative mode from the facts of phylogeny—hence, the various "laws"—Cope's, Williston's, Dollo's—of the classical literature. Simpson turned this procedure around. Instead of an exhaustive tome in documentation, he wrote 217 pages of stimulating suggestions. He started from the principles of neontological Darwinism as he saw the theory emerging. He then asked if major features of the fossil record could be reconciled to this modern version of Darwinism, without postulating any special macroevolutionary theory. *Tempo and Mode* contains 36 figures, but only one portrays an animal—actually only the lower second molar and fourth premolar of the Eocene condylarth *Phenacodus*, cribbed from Osborn (ref. 10, figure 9, p. 43). The rest are graphs, frequency distributions, and pictorial models. No paleontological innovation could have been more stunning than this.

But the most innovative feature of all resides in Simpson's well-chosen title, for he properly selected tempo and mode as the two paleontological subjects that might provide novel theory, and not just phenomenology, to the evolutionary sciences. His title is, therefore, a statement about paleontological relevance, a defense of the theoretical importance of those ten billion rats.

There is much, of course, that paleontology cannot do—based on imperfection of the record, and our imposed inability to observe or manipulate past processes directly. But, in specifying tempo and mode, Simpson sought to isolate and feature the theoretically tractable subjects of paleontology. His argument is both simple and elegant: paleontology has unique access to questions of evolutionary tempo, which require the direct data of long durations. These paleontological tempos can and should be quantified to attain a testable generality transcending the "feel" and expertise of taxonomic specialists on given groups.† Rigorous and quantitative studies of tempo (or pattern) can lead to inferences about modes (or processes). Scientific theory is, essentially, the attempt to explain nature's processes. By using uniquely paleontological data about pattern to infer the unseeable processes of long temporal spans, paleontology may be an active purveyor of evolutionary theory.

This strategy of using uniquely paleontological data about tempo to infer mode, and thus to develop theory directly from the domain of macroevolution, pervades Simpson's book and underlies all his examples. To cite just two cases:

(*i*) Designation of the three modes. Simpson's last, and best-known, chapter (ref. 10, pp. 197–217) uses data of tempo to propose a fundamental division of evolutionary processes into three modes, each with different meaning: *speciation* for a low-level process of iterating diversity, with no significant input to trends or other larger-scale patterns; *phyletic evolution* for the ordinary style of directional change, leading to evolutionary trends and accounting for some 90% of paleontological data; and *quantum evolution* for rapid and rare, but efficacious, "all-or-nothing" transitions from one adaptive zone to another through an inadaptive phase (a process analogized with Wright's model of genetic drift).

(*ii*) The theory of horotely, tachytely, and bradytely. This fascinating and brilliant, if ultimately flawed, theory has been widely misunderstood by people who do not grasp Simpson's central strategy of using tempo to infer mode. Many critics have stated that Simpson only invented some arcane, Greek-based jargon to divide the ordinary continuum of evolutionary rates into slow (brady), ordinary (horo), and fast (tachy). Not at all. Simpson was trying to identify separate peaks (modes in the statistical sense) in the distribution of tempos in order to specify distinct modes (in the ordinary sense) of evolution. Thus, horotely is not the central tendency of a single distribution of rates (with tachytely as the right tail, and bradytely as the left tail, as in the conventional misinterpretation); horotely is the *entire distribution* of ordinary rates, while tachytely and bradytely are, in Simpson's hypothesis, smaller distributions with distinct central tendencies at much larger and much smaller values than the central tendency of the horotelic distribution.

Simpson based this hypothesis upon a fascinating treatment of data on generic longevity. He contrasted extant with extinct genera by plotting longevities as conventional survivorship curves. Extinct genera fit the ecological models without anomaly, but extant genera yielded a hump of "too many" values at extended longevities—in other words, too many living bivalve genera had inhabited our planet for too long according to random models of survivorship. Simpson called this hump the bradytelic distribution. (The tachytelic

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distribution then emerged as a theoretical concept for a spectrum of rates too rapid to be recorded in most geological circumstances, and therefore responsible for the notorious gaps of the fossil record, even in relatively complete stratigraphic sections.)

Following his usual argument, Simpson then tied each of the three distributions of tempos to distinct modes of evolution—horotely to ordinary anagenesis in phyletic evolution (responsible, he argues, for some 90% of the fossil record), tachytely to quantum evolution, and bradytely to establishment of stable forms (often called "living fossils") in persistent adaptive zones. As a testimony to his proper restriction of science to the operational, Simpson said little about tachytely (which can rarely be measured and must be inferred from gaps in the record), basing his entire conception upon an attempt to identify and quantify the tractable bradytelic distribution through analysis of survivorship data, as described above.

Simpson's general argument is both illuminating and correct: tempos are a unique paleontological domain; modes may be inferred from them, and status as a source for theory thus conferred upon paleontology. Why, then, did Simpson's work fail to establish such a role for the fossil record and not lead to an independent body of macroevolutionary theory—as the deprecatory quotes cited in section one of this paper, all postdating *Tempo and* Mode, demonstrate? Two reasons can resolve this only apparent paradox:

(*i*) The dilemma imposed upon paleontology by the Synthesis. The second phase of the Synthesis had a central theme—to bring each traditional subdiscipline of natural history under the explanatory rubric of the first phase, by showing that all results could be rendered consistent with population genetics and Mendelian principles of microevolutionary change. Since paleontology had the oldest and deepest tradition for denying such a claim, and asserting the need for principles contrary to Darwinism in explaining evolution in the fullness of time (orthogenesis, various forms of vitalism and finalism), Simpson felt especially compelled to argue that the entire past, in all magnitude and duration, could be fully encompassed by extrapolation from microevolutionary principles of the moment—Darwinian uniformitarianism in its purest form.

Thus, although Simpson did enunciate a methodology—modes from tempos—for discovering uniquely macroevolutionary theory, he applied the procedure to deny this possible outcome. In other words, he developed a method that might have yielded theory, and then claimed that none was to be found. And this conclusion was no passive or subsidiary result of other purposes, but the central goal—and, in Simpson's view, the intellectual triumph—of his work. Paleontology became a dutiful son to the synthesis, and no longer an unruly child. Simpson concluded, with evident satisfaction (ref. 10, p. 124):

> The materials for evolution and the factors inducing and directing it are also believed to be the same at all levels and to differ in mega-evolution only in combination and in intensity. From another point of view mega-evolution is, according to this theory, only the sum of a long, continuous series of changes that can be divided taxonomically into horizontal phyletic subdivisions of any size, including subspecies.

(*ii*) Simpson's later moves to greater conventionality. Of his three evolutionary modes, Simpson always emphasized the one—phyletic evolution—most supportive of extrapolationism, for trends in the phyletic mode work by pure, step-by-step anagenetic accumulation, the "march of frequency distributions" through time. He exalted the phyletic mode as primary by two strategies. First, by asserting the predominant relative frequency of this maximally extrapolationist mode—the 9/10 figure previously cited: "Nine-tenths of the pertinent data of paleontology fall into patterns in the phyletic mode" (ref. 10, p. 203).

As a second strategy, he downplayed the other two modes. He saw speciation as a low-level process, capable only of producing iterated variety (and perhaps of protecting adaptations by sorting them into several lineages), but not as participating in sustained evolutionary trends: "This sort of differentiation draws mainly on the store of preexisting variability in the population. The group variability is parceled out among subgroups. . . . The phenotypic differences involved in this mode of evolution are likely to be of a minor sort or degree. They are mostly shifting averages of color patterns and scale counts, small changes in sizes and proportions, and analogous modifications" (ref. 10, p. 201).

But quantum evolution posed a different challenge to the dominance of phyletic extrapolationism. Simpson had never granted quantum evolution a high relative frequency, but he did regard this mode as responsible for some of the most profound anatomical transitions in life's history. In *Tempo and Mode*, Simpson did present quantum evolution as an alternative to the phyletic mode, with different primary causes (though still tolerably uniformitarian in invoking Wright's genetic drift). But Simpson radically changed his view in his larger, and far more conservative, later book, *The Major Features of Evolution* (12). He now demoted quantum evolution from a separate mode to merely an extreme value in the phyletic spectrum. He began by denying any efficacy to Wright's process: "Genetic drift is certainly not involved in all or in most origins of higher categories, even of very high categories such as classes or phyla" (ref. 12, p. 355). He then redefined quantum evolution as one among four styles of phyletic evolution, all characterized by "the continuous maintenance of adaptation" (ref. 12, p. 385). Quantum evolution was therefore transmogrified from a distinct mode to extrapolative accumulation of adaptive change at fastest rates: Quantum evolution, he now claimed, "is not a different sort of evolution from phyletic evolution, or even a distinctly different element of the total phylogenetic pattern. It is a special, more or less extreme and limiting case of phyletic evolution" (ref. 12, p. 389).

I see a kind of supreme irony in Simpson's argument and its ontogenetic development. He made a brilliant and expansive move in recognizing that paleontology had access to theory through the quantification of tempos and inference of modes. But he then found no theory where it might have resided, and he became ever more wedded to the synthetic proposition that all in time's vastness could be rendered by extrapolation from Darwinian processes seen in the genetics of modern populations. Paleontology therefore remained the subsidiary playing field for a game with rules fully specified elsewhere. Simpson hoped to win respect for paleontology by defining his field as an ally to the synthesis but, as in politics and war, faithfulness without independence will be used to the utmost, but never really honored with equality.

A Solution in Bonded Independence

Dichotomy is both our preferred mental mode, perhaps intrinsically so, and our worst enemy in parsing a complex and massively multivariate world (both conceptual and empirical). Simpson, in discussing "the old but still vital problem of micro-evolution as opposed to macro-evolution" (ref. 10, p. 97), correctly caught the dilemma of dichotomy by writing (ref. 10, p. 97): "If the two proved to be basically different, the innumerable studies of micro-evolution would become relatively unimportant and would have minor value for the study of evolution as a whole."

Faced with elegant and overwhelming documentation of microevolution, and following the synthesists's program of theoretical reduction to a core of population genetics, Simpson opted for denying any distinctive macroevolutionary theory and encompassing all the vastness of time by extrapolation. But if we drop the model of dichotomous polarization, then other, more fruitful, solutions become available.

The Synthesis arose in a reductionistic age, as best evidenced by the contemporary "unity of science" movement initiated by philosophers of the Vienna Circle (see ref. 13, for a fascinating account of these links), and by the general intellectual context now called modernism, and then so dominant in a variety of fields from architecture to classical music. Modernism's emphasis on the abstract, the simplified, the fully universal, the underlying principles that build the unique and complex from the small and general, all fueled the preference within evolutionary biology for a comprehensive micro-level theory that could build all scales and sizes by smooth extrapolation. Theory introduced at the macro-level seemed antithetical—a true dichotomous contrary—to such a program.

We now live in an age of self-styled "postmodern" reformation—and though this movement has engendered silliness in architecture and incomprehensibility in literature, postmodernism has also greatly benefited intellectual life by stressing themes of pluralism, multi-level causality, virtues of complexity, individuality, and, yes, even a bit of playfulness. Modernism's hegemonic idea of universal reduction to lower-level principles and causes has been replaced by respect for the legitimacy of multiple levels and perspectives and for their causal mechanisms and insights.

In this postmodern context, it should be easy to grasp a stunningly simple and utterly unprofound solution to "the old but still vital problem of microevolution. . . [and] macroevolution." (But you do need the context to see the "obvious," hence the unavailability of this solution under modernism.) I put an ellipses in Simpson's statement to eliminate the three words that cause all the trouble—"as opposed to." Micro- and macroevolution are not opposed, but neither does one follow by extrapolation from (and therefore become intellectually subservient to) the other. The existence of genuinely independent macroevolutionary theory does not imply that "the innumerable studies of micro-evolution would become relatively unimportant." These studies are vitally important both as controlling in their own domain, and powerfully contributory to macroevolution as well. Contributory, but neither exclusive nor decisive. No dichotomy exists. There is no single pathway of reductive explanation. Our evolutionary world is a hierarchy of levels, each of legitimacy and irreducible worth. I propose no California love-fest of "I'm OK, you're OK." Genuine pluralism is tough minded and rigorous in trying to map theoretical complexity upon our hierarchical world. Empiricism adjudicates, and some levels may turn out to be unimportant in nature, though plausible in theory. But we must entertain the legitimacy of all logically coherent levels in order to find out.

In seeking an independent body of macroevolutionary theory, not construed as contrary to microevolutionary knowledge, but viewed as truly complementary in bonding to produce a more satisfying total explanation, I would focus upon two themes that share the common feature of rejecting Darwin's uniformitarian extrapolationism, not his natural selection (or other major meanings of Darwinism).

(*i*) Causal boundaries between levels, breaking the possibility of smooth upward extrapolation. Darwin's uniformity requires isotropy in extension, all the way from low causal to high phenomenological; nothing in the structure of causation may break the ever-growing inclusion. But if, on the other hand, important new causes arise at higher phenomenological levels of long time or great magnitude—even if most of the results be complementary to those produced by lower-level causes (though they need not be congruent, and may well be contrary or orthogonal)—then the extrapolationist paradigm is invalid.

I believe that nature is so hierarchically ordered in a causal sense and that distinct processes emerge at a series of ascending breakpoints in time and magnitude. To mention the two themes that have been most widely discussed in paleontological literature during the past twenty years:

(*a*) Punctuated equilibrium and trends within clades. Trends in the anagenetic mode may be understood as pure extrapolation and accumulation by selection (or other processes) operating at sequential moments in populations. But if species tend to be stable after geologically momentary origins, as punctuated equilibrium proposes (see ref. 14 for a best case, ref. 15 for a compendium of support, and refs. 16 and 17 for opposition), then trends must be described as the differential success of certain species within a clade (as a result of greater longevity, higher propensity to speciate, or biased direction of speciation)—and the reasons for geological success of species are both intrinsically macroevolutionary, and distinct from accumulation by natural selection within a continuously evolving population. Moreover, if the characters causing differential species success are emergent properties of species themselves (18), then the reasons for macroevolutionary change by species selection within clades are formally irreducible to conventional Darwinian selection upon organisms within populations.

(*b*) Mass extinction and patterns of waxing and waning among clades. Darwin, as noted above, feared and rejected mass extinction [see Raup's article in this symposium (19)]—not because such coordinated dying is inconsistent with natural selection (for nothing in this form of Darwinism guarantees that organisms can adapt to environmental change of such magnitude and rapidity), but because mass extinction breaks the extrapolative causal continuum that the uniformitarian meaning of Darwinism requires. Mass extinctions are not random, but survival through them works by different rules (see ref. 20 for a general argument, ref. 21 for an intriguing example) from those that regulate success in Darwinian struggles of normal times. Darwinian accumulation through normal times cannot, therefore, encompass the history of life. If mass extinctions only accelerated, but otherwise coincided in causal direction with events of normal times (the "turning up the gain" model in my terminology—ref. 22), or if mass extinctions were only minor patterning agents, then the extrapolative Darwinism of normal times would still rule. But mass extinctions are not coincident, and they are truly massive (up to 96% species death of marine invertebrates in a well-known estimate for the largest, late Permian great dying ref. 23). They are, therefore, causal patterning agents separate from the daily Darwinism of normal times.

(*ii*) The hierarchical reconstruction of the theory of natural selection. Darwin's key notion, that natural selection works almost entirely upon individual organisms as primary units, arises from several aspects of his thinking—from, for example, his uniformitarianism (for organisms are the noticeable biological objects of moments), and his overthrow of Paleyan teleology. (What a delicious irony—to claim that good organic design and ecological harmony, once seen as proof of God's wise benevolence, truly arise only as the side consequence of a process with apparently opposite ethical meaning—organisms struggling for their own benefits alone, defined as individual reproductive success.) Classical Darwinism, as a single-level theory causally focused upon organisms, makes sense in traditional terms (while the attempt of Dawkins and others to reduce the level of causality even further to genes can only be called hyperdarwinism, or more of the same; see ref. 24). Williams (ref. 25, p. 6) correctly identifies conventional Darwinian methodology: "In practice, higher levels of selection are seldom invoked, and biologists routinely predict and find that the properties of organisms are those expected if selection operates mainly on the varying capabilities of individuals."

In this context, I believe that the most portentous and far-ranging reform and expansion of Darwinism in our generation has been the growing (26–28), if so far ill-coordinated, attempt to reconstruct the theory of natural selection as a more general process, working simultaneously on biological objects at many levels of a genealogical hierarchy. The revised theory is in no way antithetical to Darwinian natural selection and should be read as an extension rather than a replacement. But the hierarchical theory has a structure very different from conventional, single-level Darwinism working on individual organisms—so the revised theory is a fascinating novelty, not a more inclusive extrapolation. After all, there is a world of difference between the claim that nature's momentarily stable objects are optima or maxima set by one canonical form of selection and the statement that such stabilities are balances among distinct levels of selection that may work coincidentally, orthogonally, or contrarily. Since most of these newly recognized levels are intrinsically macroevolutionary (species selection, clade selection, and some forms of interdemic selection), and since their ways and modes are distinct from conventional natural selection on individuals, the hierarchical theory also affirms a substantial theoretical space for macroevolution and its paleontological basis.

To be a unit of selection, biological objects must embody five basic properties: birth points, death points, sufficient stability through their existence, reproduction, and inheritance of parental traits by offspring. (The first three properties are required to individuate any named item as a distinct entity rather than an arbitrary segment of a continuum; the last two are prerequisites for agents of Darwinian selection, defined as differential reproductive success.) Organisms are the quintessential biological objects endowed with these five properties, hence their role as canonical Darwinian individuals in the basic theory.

But many other kinds of biological objects maintain these five properties, and can therefore act as causal agents of selection. The hierarchical theory is therefore explicitly causal, and not merely phenomenological. We may start with gene selection—not the false Dawkinsian version, which tries to break all higher-level processes down to this supposedly universal locus of causality, but the proper form of genes acting "for" themselves, as in the badly named phenomenon of "selfish DNA" (29, 30). (In the general theory of selection, all objects work for themselves by struggling for differential reproductive success at their own level; multiply replicating DNA, producing no benefits to organisms thereby, can only be viewed as selfish if all evolutionary change be judged by impact upon organisms—the very Darwinian parochialism now superseded by the hierarchical theory!)

Moving up a level, Buss (31) has made a fascinating case for a distinct form of cell-lineage selection, with cancer as one mark of its pyrrhic victory over conventional selection on organisms. We next encounter ordinary Darwinian selection on organisms, a powerful mode surely responsible for adaptive design of bodies [but not, therefore, *pace* Dawkins (32), more intrinsic or more important than other evolutionary phenomena, like waxing and waning dominance among clades through geological time—a phenomenon that surely cannot be fully rendered by differential merits of adaptive design among organisms].

Moving to levels above organisms, we first encounter the confusing field of selection among groups or demes within species—a theme once infused with woolly thinking (ref. 33, for historically needed correction) that gave the entire subject a bad name, but now being treated more rigorously and surely containing much of enormous value in various modes termed interdemic, trait-group, etc. (34, 35). Above this complex field, we encounter the two clear levels of truly macroevolutionary selection, largely based upon paleontological data, and capable of producing important phenomena of evolutionary pattern not fully rendered by causes at lower levels—species selection (36–38) for trends within clades and clade selection (25) for differential waxing and waning of monophyletic groups.

The developing field of hierarchical selection theory is beset with conceptual difficulties so thorny that I sometime wonder if our innately dichotomizing minds are sufficiently well constructed for thinking about simultaneous levels interacting in all possible modes (or perhaps I'm just stupid, although the issues seem to beset others as well). Two problems have been paramount in the developing discussion.

(*i*) How shall selection itself be identified and defined? Since we desire an explanatory theory, we must clearly distinguish (18) the causal process of selection (differential survival based on active and intrinsic properties of the biological objects under review), from the descriptive phenomenon of sorting (differential survival that might be causally based upon selection at lower or higher levels, yielding sorting as an effect). Even with this proviso, several partly contradictory criteria for the definition of selection as a causal process at higher levels have been proposed. Most firm and unambiguous, but most elusive and hard to document, is the "emergent trait" approach (18, 37), where selection is only identified if explicit features responsible for sorting can be specified as emergent in the objects being sorted. Differential success based on emergent traits is surely selection by anyone's definition and permits us to speak of genuine adaptation at higher levels—but emergent traits may be rare, and are surely hard to define, often demanding narrative knowledge of selective processes not available from data of fossils.

The "emergent fitness" approach (39) is more general and operational (through use of ANOVA-type models applicable to quantitative data of fossils), but fitnesses are not traits, and the analog to adaptation is thereby lost, along with clear correspondence to vernacular notions of "advantageous." This approach does, however, provide the enormous advantage of including selection upon variability as a legitimate form of causality at higher levels.

Williams (25) has proposed an even more inclusive definition for clade selection, an interesting position for a man who formerly criticized all proposed forms of group selection so brilliantly, and who became identified thereby as a champion of lower-level selection (33). Williams seems to define as higher-level selection any form of sorting between groups that can be described as nonconcordant with any simultaneously observed mode of sorting at the organism level (see his interesting hypothetical example in ref. 25, pp. 50–52).

(*ii*) How shall the items and units of selection be identified and defined? Two major contributors to this debate on hierarchical selection—Eldredge (40) and Williams (25)—have tried to establish parallel hierarchies of equal causal import: genealogical and ecological for Eldredge, material and codical for Williams. I believe that these efforts are ill-advised and that only the genealogical and material sequences should be viewed as causal units participating in Darwinian selection.

Williams makes his distinction between entities and information, speaking (ref. 25, p. 10) of "two mutually exclusive domains of selection, one that deals with material entities and another that deals with information and might be termed the codical domain." But I do not think that the codical domain has meaning or existence as a locus for causal units of selection, for two reasons:

(*a*) Odd mapping upon legitimate intuitions. Williams uses a criterion of selection that arises from an important literature developed by Hull (41), Sober (42), and others on replicators and interactors—and that requires relatively faithful replication across generations in order to qualify an entity as a unit of selection. (Sexual organisms, dispersed and degraded by half in each offspring of the next generation, do not qualify on this criterion—a major argument advanced by gene selectionists for locating causality instead at the lower level of faithfully replicating sequences of DNA.) Williams accepts this criterion for his codical domain, thus leading to the following peculiar position: *genes* are units of selection (as the replicating consequence in the codical domain of selection upon organisms in the material domain); *gene pools* are also units of selection (as replicating consequences of higher-level selection upon groups to clades); whereas *genotypes*, in an intermediate category, are *not* units of selection (except in asexual organisms, where replication is faithful). Thus the codical domain skips a space in the hierarchy, and contains no organismic level of selection (except for asexual forms) because the corresponding codex is impersistent.

This linkage of selective agency to faithful replication has been so often repeated in the past decade that the statement has almost achieved status as dogma in evolutionary theory. Yet I think that this criterion is entirely wrong. Selection isn't about unitary persistence—never was, and never should have been so formulated. Selection is about concentration—that is, the differential passage of more of "youness" into the next generation, an increase in relative representation of the heritable part of whatever you are (whether you pass yourself on as a whole, or in disaggregated form into the future of your lineage). Consider the standard 19th Century metaphor for selection: a sieve. The sieve is shaken, and particles of a certain size become concentrated, as others pass through the net (lost by selection). Integral "you" may be disaggregated in this process, but so long as the next generation contains a relative increase in your particles, and so long as you qualified as an active causal agent of the Darwinian struggle while you lived, then you are a unit of selection (and a winning unit in this case).

(*b*) The codical domain as bookkeeping only. We may indeed, and legitimately as a practical measure, choose to keep track of an organism's success in selection by counting the relative representation of its genes in future generations (because the organism does not replicate faithfully and therefore cannot be traced as a discrete entity). But this practical decision for counting does not deprive the organism of status as a causal agent, nor does it grant causality to the objects counted.

The listing of accounts is bookkeeping—a vitally important subject in evolutionary biology, but not a form of causality. I think that Williams's codical domain is not an alternative realm of causality, as he claims, but just a fancy name for the necessary bookkeeping function of evolutionary calculation. Williams almost seems to admit as much in two passages (ref. 25, pp. 13 and 38):

> For natural selection to occur and be a factor in evolution, replicators must manifest themselves in interactors, the concrete realities that confront a biologist. The truth and usefulness of a biological theory must be evaluated on the basis of its success in explaining and predicting material phenomena. It is equally true that replicators (codices) are a concept of great interest and usefulness and must be considered with great care for any formal theory of evolution. (ref. 25, p. 13)

Fine. But codices are units of information useful in bookkeeping, not material entities "out there" in the Darwinian struggle—and bookkeeping is not causality.

However we ultimately define the levels in a genealogical hierarchy of effective selection upon each, and however we decide to codify the criteria for identifying selection at these levels, the hierarchical, multi-level theory of natural selection should put an end to an unhappy and unhelpful conflict rooted in the false mental tactic of dichotomization: the modes of macro- and microevolution as intrinsically opposed and in battle for a common turf. This model led the Synthesis to deny any theoretical status to macroevolution at all—thus preserving hegemony for a microevolutionary theory that could supposedly encompass all scales by smooth extrapolation. But macroevolution is complementary, not oppositional—and each domain holds unique turf (while maintaining a rich and fascinating interaction with all other realms). A grant of independence and theoretical space to a previously rejected domain does not mark a retreat or a submission, but rather a commitment to probe all the richness of nature with all the mental equipment that our limited faculties can muster. For a fine poet once stated this "Happy Thought" in *A Child's Garden of Verses*:

> The world is so full of a number of things,
> I'm sure we should all be as happy as kings (43).

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North American Journal of Fisheries Management 14:99–111, 1994

Diel Habitat Selection by Brown Trout in the Rio Grande River, Colorado, after Placement of Boulder Structures

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Abstract.—Brown trout *Salmo trutta* distribution and microhabitat use were measured in 10 study sections of the Rio Grande River, Colorado, where three types of structures made from large boulders had previously been placed. On average, 65% of the adult brown trout and 69% of the juvenile brown trout observed were holding positions near structures. Brown trout used primarily wingdams, midchannel boulder clusters, and natural bank cover, and avoided single boulders and areas with no structures. Juvenile and adult brown trout showed a significant preference for wingdams during the day at both high and low flows, but adults shifted from wingdams to midchannel boulder clusters at night during low flows. Distributions of water depth and mean water velocity at positions used by brown trout differed significantly between age-classes but were generally not significantly different at high versus low flows, between day and night, or between fish using and not using structures. Results suggest that brown trout selected feeding sites primarily based on water velocity and cover, and that boulder structures provided more locations that were energetically favorable for brown trout.

The lack of suitable physical habitat in many streams and rivers is thought to limit fish abundance, growth, and survival (White 1986). When faced with this lack of appropriate habitat, fishery managers often evaluate potential habitat deficiencies and prescribe stream habitat enhancement to improve conditions. Knowledge of microhabitat requirements of fish, and an understanding of how enhancement structures modify the physical environment, are essential for project success.

Despite the widespread use of habitat enhancement, few investigators have studied stream channel morphology and trout distribution after habitat structures were installed to determine whether more favorable positions were created and whether trout used them. Instead, the majority of postproject evaluations have focused on population responses (e.g., Hunt 1971, 1992), which may require 5–7 years to reach their full extent (Hunt 1976). Moreover, with few exceptions (e.g., Ward and Slaney 1981; Hunt 1988), investigators have not compared the relative use of various structure designs by fish, and none have compared use of structures during day versus night.

In this study we examined whether boulder structures placed in a southern Colorado river influenced diel distribution and microhabitat use of brown trout *Salmo trutta* over a range of streamflows. Our objectives were first to determine if boulder structures of three designs influenced diel position choice of brown trout and whether this position choice changed with streamflow or fish life stage. Second, diel microhabitat use, as characterized by water depth, mean water velocity, and cover, was measured for brown trout associated and not associated with structures, to assess which microhabitat attributes were most important in determining position choice.

Study Area

The Rio Grande River, in southwestern Colorado, is a fourth-order river (Strahler 1952) with headwaters originating in the San Juan Mountains. Our study area was a 3.8-km reach in the Coller State Wildlife Area (CWA; map location: T40N,

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R2E, sections 11–13), 8 km west of South Fork, Colorado, at an elevation of 2,560 m. Mean monthly discharge during the 1989–1991 water years ranged from 2.8 m^3/s during late fall and winter base flow to a maximum of 59.7 m^3/s during spring snowmelt runoff (Ugland et al. 1990, 1991, 1992). Flows during the 1989, 1990, and 1991 water years were 89, 92, and 107% of the long-term average. A reservoir about 65 km upstream from the CWA was dewatered for repairs during summer 1990, so flows were unregulated. However, rainfall eroded fine sediment from the reservoir bed and caused increased turbidity. Summer water temperatures ranged from 6 to 17°C (R. B. Nehring, unpublished data for 1982–1984 and 1990).

The study reach had predominantly low-gradient riffles and runs with small to large cobble substrate. Mean channel width was 55 m, and sinuosity was approximately 1.2. The reach was relatively devoid of boulders and debris jams, probably due to log and railroad tie drives from about 1875 through 1915 (V. Spero, U.S. Forest Service, personal communication).

In 1978 the Colorado Division of Wildlife began a large-scale habitat enhancement program by adding boulders to the channel. Single boulders, midchannel horseshoe-shaped boulder structures (three to five boulders, concave downstream), and boulder bank deflectors (12–15 boulders in a line that angled downstream, hereafter called wingdams) were placed throughout the CWA in November 1978, 1982, and 1985. Altogether, 883 boulders, 1–2 m in diameter, were placed in the channel at a cost of $57,000. Midchannel boulder clusters covered 3–6% of total channel width, whereas wingdams covered 6–20%. In 1985, eight boulder–log combination structures were also installed, but the logs broke loose and washed away during snowmelt runoff. Flows during 1987, which were among the highest on record (170% of average), scoured pools downstream from the boulder structures and created the habitat conditions present during the study.

From 1981 to 1991, the salmonid assemblage in the CWA consisted primarily of wild brown trout and a lesser number of wild rainbow trout *Oncorhynchus mykiss*. For example, the population of age-1 and older fish in mid-November 1990 was estimated as 4,144 brown trout and 702 rainbow trout throughout the CWA (Nehring, unpublished). Density estimates of trout 35 cm or longer were 27 brown trout and 3 rainbow trout per hectare. Longnose dace *Rhinichthys cataractae* and a few large white suckers *Catostomus commersoni* were also present.

Special regulations requiring anglers to release all trout less than 400 mm long had been in effect in the CWA since 1983. However, only a few brown trout that lived to age 6 reached 400 mm in the CWA (Nehring, unpublished), so angling mortality was low. Angling occurred primarily during June through August, but effort was low (<250 h/hectare/year; Nehring, personal observation), so fishing had little effect on trout populations.

Methods

In spring 1989, the 3.8-km reach was divided into 50 sections, each 75 m long. Sections were categorized as having high (>40 boulders), medium (21–40 boulders), or low density (≤20 boulders) of habitat structures based on the total number of boulders. Three study sections were randomly selected from each category. An additional low-density section, which had only one structure, was added in 1990. Habitat in this tenth section was similar to that throughout the reach before boulder placement. Gradient ranged from 0.1 to 0.4% among the 10 sections.

In all, 85 transects were used to quantify physical changes caused by structures in the study sections during summer 1990. More transects were placed in sections with high structure density than in low-density sections. Total depth (cm), mean water velocity (cm/s) at 0.6 depth from the surface, and substrate (modified Wentworth classification; Orth 1983) were measured at 1.5-m intervals across transects.

Measuring Trout Positions

Locations of juvenile and adult brown trout and rainbow trout were determined by underwater observation during day and night from July through September 1990. Angling was also used to determine daytime locations of feeding fish when underwater visibility was less than 1.0 m. Maximum underwater visibility was greater at night (approximately 3.0 m) than during the day (1.5–2.0 m) due to scattering of sunlight by suspended fine particles (Fausch and White 1981). As a result, during the day trout were often more easily located from above the water surface than by snorkeling. The small number of rainbow trout observed during the study ($N = 56$) precluded analysis, so the data are not reported here.

Underwater observation procedures were similar to those of Bovee (1986) and Li (1988). A static-line, drop-line system with mountaineering

Oecologia (1994) 100:1–12

ORIGINAL PAPER

Bob –
Thanks for your review.
Kurt

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Distribution of two congeneric charrs in streams of Hokkaido Island, Japan: considering multiple factors across scales

Received: 17 January 1994 / Accepted: 15 June 1994

Abstract *Salvelinus leucomaenis* (white-spotted charr) and *S. malma* (Dolly Varden) are distributed throughout Hokkaido Island, Japan, but sites where they occur in sympatry are rare. In general, *S. malma* inhabit upstream reaches and *S. leucomaenis* extend downstream to the ocean. Factors influencing their distribution were analyzed at four spatial scales ranging from the whole island to individual stream pools. At the island scale, *S. leucomaenis* were found in the warmer south-west region and at lower altitudes elsewhere, whereas *S. malma* were found in the colder north-east and at higher altitudes. At a regional scale, the downstream limit of *S. malma* and upstream limit of *S. leucomaenis* shifted to lower altitude from south-west to north-east across the island, coincident with the decrease in temperature. Further analysis showed that transition points from *S. leucomaenis* or sympatry to *S. malma* in individual watersheds were closely related to an index of cumulative mean monthly temperatures exceeding 5°C. However, at the scale of a single watershed, the transition occurred at different altitudes, gradients, and temperatures in two tributaries, apparently because stream discharge, habitat, and disturbances from floods interacted with these abiotic factors to limit distribution. The two charr species developed interspecific dominance hierarchies in individual pools, and there was strong complementary density compensation among stream pools that could be explained by interspecific competition but not by differences in habitat. However, patterns at watershed and regional scales suggested that interspecific competition interacts with temperature in complex ways. We conclude that the importance of various abiotic and biotic factors in shaping Hokkaido charr distributions depends on the scale at which they are viewed.

Key words Multiple factors · Scale · Altitudinal distributions · Temperature · Interspecific competition

Introduction

Ecologists have long been intrigued by distributions of closely related species in vertebrate communities that are arrayed along altitudinal gradients, where abiotic factors and species composition change quickly over short distances (Hairston 1949; Diamond 1970; Terborgh 1971; Schluter 1982; Brown and Bowers 1984). Congeneric species in such communities are often found to occupy adjacent, non-overlapping positions along the gradient, and to expand their distribution at locations where their congener is absent, patterns that are frequently interpreted as evidence for interspecific competition (e.g., Terborgh and Weske 1975; Diamond 1978). Rarely, however, have alternative hypotheses for the distributions been considered (Wiens 1989a; but see Schluter and Grant 1982).

In reality, limits of species distributions are influenced by a host of factors that combine or interact to produce the patterns found in nature (Hall et al. 1992; Table 1). Progress in understanding the multiple factors that limit species distributions on altitudinal gradients will most likely be made by considering each as an alternative hypothesis to be tested using data on relevant abiotic and biotic variables (Wiens 1989a). Moreover, because different factors may operate at different spatial and temporal scales (e.g., Wiens 1986; Bennett 1990), multi-scaled investigations are required to place the role of each into an appropriate context (Wiens 1989b).

Like other taxa, salmonid fishes in streams show complementary distributions along altitudinal gradients in

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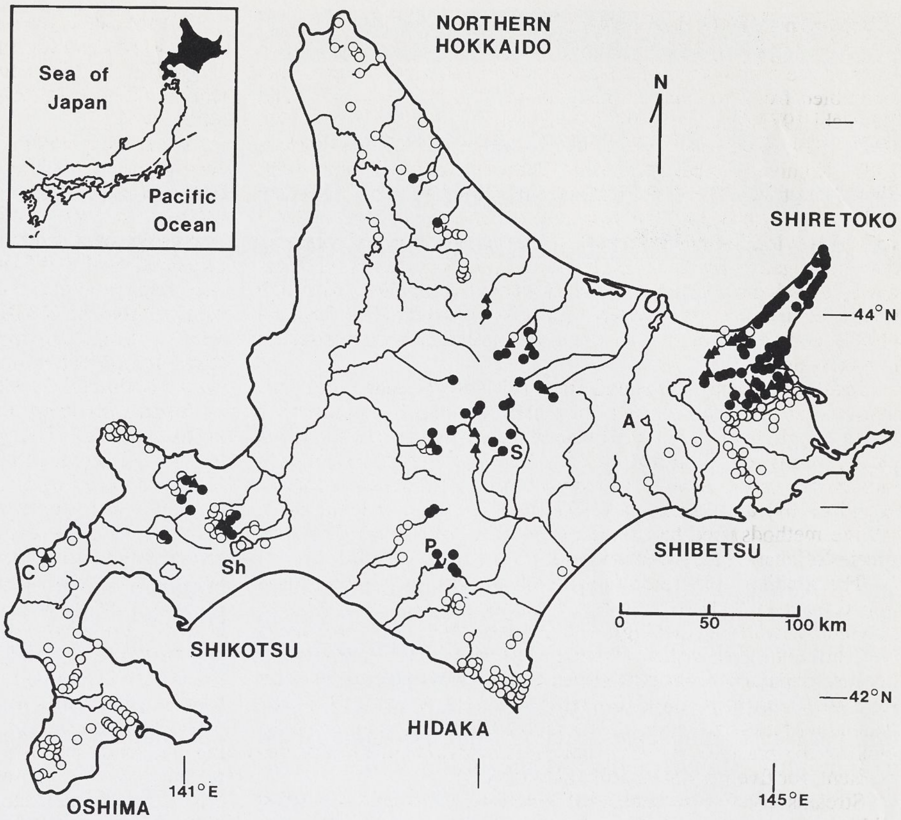

Fig. 1 Map of Hokkaido Island, Japan, showing sites at which *Salvelinus malma* (*filled circles*), *S. leucomaenis* (*open circles*), and both species in sympatry (*filled triangles*) were present. In some regions many sites with the same species composition overlapped, so to improve clarity not all are shown. Locations of the Chihase River (*C*), Lake Shikotsu (*Sh*), Poroshiri watershed (*P*), Lake Shikaribetsu (*S*), and Lake Akan (*A*) are also shown. The *dashed line* through Honshu Island on the inset of Japan is the southern limit of *S. leucomaenis* distribution. *Names* refer to regions discussed in the text

many parts of the world (e.g., Ishigaki 1969, 1984; Vincent and Miller 1969; Gard and Flittner 1974; Larson and Moore 1985; Fausch 1988, 1989). In many cases, one species occupies the high-gradient headwater reaches at higher altitudes whereas another inhabits lower-gradient reaches downstream, often with little overlap (Fausch 1989). Often the downstream species is an exotic salmonid that has gradually encroached upstream, forcing the native species into headwater habitat (e.g., Townsend and Crowl 1991). Rarely have distributions of native congeneric salmonids been studied, however (but see Hartman and Gill 1968).

Here we analyze distributions of two closely related native congeneric charrs (genus *Salvelinus*) in streams of Hokkaido, the northern island of the Japanese archipelago. We present data at four spatial scales, ranging from the whole island to individual stream pools, and relate distributional limits to relevant abiotic factors and the presence of the other species. The results of these analyses are used to show how certain factors vary in importance, and interact, across spatial scales, and to suggest others that appear unlikely to strongly affect distributions of the two species.

Background and methods

Zoogeographic distribution

The worldwide distribution of *S. leucomaenis* (white-spotted charr) is from the Kie Peninsula in Honshu, the main island of the Japanese archipelago (Fig. 1), north to the Okhotsk Sea and Kamchatka Peninsula (Ishigaki 1984; Kawanabe 1989; Chereshnev 1991). The distribution of its congener, *S. malma* (Dolly Varden) is from southern Hokkaido north around the Pacific rim to Puget Sound, Washington (Armstrong and Morrow 1980; *S. malma* reported from all but one site farther south in North America were *S. confluentus*, Cavender 1978). Thus, the two species overlap in distribution from Hokkaido north to Kamchatka. They belong to the same subgenus of *Salvelinus* (Behnke 1989), are morphologically similar, and phylogenetically closely related (Cavender 1989; Murata et al. 1993).

Table 1 Factors that may limit distributions of charr in Hokkaido (modified and extended from Wiens 1989a)

1. Historical factors (e.g., evolution, speciation)
2. Barriers that prevent dispersal
3. Climatic factors producing physiological stress
4. Lack of suitable habitat
5. Area too small to support viable population
6. Disturbance, via wide fluctuations in physico-chemical factors
7. Absence of a critical resource, such as food type
8. Interactions with one or more interspecific competitors
9. Predation
10. Disease or parasites
11. Chance
12. Interactions among factors

In Hokkaido, most populations of *S. leucomaenis* are largely anadromous, but also have mature male parr that reside in streams throughout life (Ishigaki 1984; Nakano and Maekawa, in press). They are, however, easily landlocked in streams within 20–30 years following construction of barriers to upstream migration. In contrast, most populations of *S. malma* are entirely fluvial. Only a few anadromous *S. malma* have been captured, almost exclusively in streams of the Shiretoko Peninsula (Hikita 1962; Ishigaki 1967; Maekawa 1973; Komiyama et al. 1982).

Distribution on Hokkaido Island

Data on the distribution of charr species in Hokkaido Island were assembled from 16 sources (Ishigaki 1969, 1984; Nakamura and Takeuchi 1973; Abe et al. 1977; Maekawa 1977; Goto et al. 1978, 1982, 1989; Komiyama 1981, 1982; Kawamura 1982; Anonymous 1987; Komiyama and Takahashi 1988; Furukawa-Tanaka 1989; Shimoda et al. 1993; S. Nakano, unpublished data collected 1989–1992). About half the data were collected by Ishigaki (1984; 153 of 360 lotic sites), and most of the rest (172 of 207 sites) by five investigators (A. Goto, H. Kawamura, E. Komiyama, K. Maekawa, S. Nakano). Seven lentic sites were also sampled. Although relative abundance was available for all sites sampled by Ishigaki (1984), and for 15 others, we used only presence/absence data in our analysis.

Most investigators captured fish with several gear types, primarily cast nets, chasing nets (a small one-man bag seine on a frame), angling gear, and hand nets. Nakano also used a backpack electrofishing unit (Smith-Root, Inc., Vancouver, Wash., USA) and underwater observation to document presence/absence, and Ishigaki (1969) and Maekawa (1977) used gill nets at lentic sites. All the methods used had a high probability of detecting the two species of charr if they were present.

The gradient and mean altitude of all lotic sites were determined from 1:50,000 scale topographic maps. Maps were also inspected for waterfalls or high-gradient cascades. Dams and weirs were not considered when assessing historical charr distributions, because populations of both species are known to persist upstream from such man-made migration barriers (Shimoda et al. 1993; Nakano and Maekawa, in press). We analyzed the distribution data by plotting the presence of both species as functions of altitude and gradient, for five regions of Hokkaido (Fig. 1).

Streams create interconnected hierarchical networks, so sites within the same watershed are not strictly independent, although nearly all sites were at least 500 m apart. This lack of statistical independence, as well as possible pseudoreplication (*sensu* Hurlbert 1984) due to considering multiple sites within watersheds, caused us to adopt a conservative approach and avoid statistical analyses. However, though not a random sample, the large number of sites (n=360) is distributed throughout most regions of Hokkaido with at least moderate topographic relief, and any bias probably favored locating reaches where the two species were sympatric, and points of transition between the two species, due to the interests of investigators (e.g., Ishigaki 1984; S. Nakano, unpublished data). Therefore, because each watershed can be considered as an independent sampling unit, we focused further analysis on points of transition from *S. leucomaenis* (or sympatry) to *S. malma* along 54 stream courses where we could estimate this from adjacent sites (Poroshiri and Migi Sawa not included). We then plotted these as functions of altitude, gradient, and a warmth index (WI) developed by Kira (1977) to explain distribution limits of plants in Japan. The index is the sum of the remainders left when 5°C is subtracted from mean monthly temperatures that exceed 5°C (e.g., during April through October near Shikotsu Lake). All sites were divided into WI classes based on 15°C isopleths shown in Yabe (1993, Fig. 2; and personal communication).

Distribution in Poroshiri Stream

During June and July of 1991 and 1992 we made detailed measurements of temperature, gradient, discharge, and charr distributions in one third-order (1:25,000 scale; Strahler 1957) stream in the Hidaka Mountain region of south-central Hokkaido (Fig. 1). Poroshiri Stream has one major tributary, called Migi Sawa (Right-hand Stream), and drains into a reservoir downstream (see Fig. 1 of Nakano and Furukawa-Tanaka 1994). Both streams have *S. malma* in allopatry in the headwaters and both species in sympatry downstream, and the life history of both species is entirely fluvial. The study area is in a remote, private watershed, so angling rarely occurred.

We measured gradient at 13 locations along the stream courses using a level and leveling rod in the field, as well as calculating it at specific locations from a 1:25,000 map. Gradients calculated from 1:25,000 and 1:50,000 scale maps were within 0.3% of each other (n=4).

Water temperature was measured at four locations during 24 June to 13 July 1992: at the upstream end of the *S. leucomaenis* distribution in Poroshiri Stream (960 m altitude) and Migi Sawa (860 m), at 860 m altitude in Poroshiri Stream for comparison with Migi Sawa, and at 785 m in Poroshiri. Temperature was also measured at the 785-m site in 1991. Temperature (0.1°C resolution) integrated over 1-h periods (2 h at 785-m site) was measured using calibrated KADEC-U recording thermographs (Kona System Co. Ltd., Sapporo, Japan) at the three upstream sites and a Ryan TempMentor thermograph at the 785-m site (Ryan Instruments, Redmond, Washington, USA).

Stream discharge was measured on 12 July 1992 at the three upstream sites (>860 m) where temperature was measured, using the U.S. Geological Survey midsection method (Orth 1983). Discharge in Poroshiri Stream typically reaches its lowest level in July, after snowmelt runoff subsides.

We determined distribution and relative abundance of charr by electrofishing, angling, cast-netting, and underwater observation. We estimated charr abundance by two-pass removal electrofishing (cf. Riley and Fausch 1992) at two sites in Poroshiri Stream (sites B and C, one pass only at C due to equipment failure; see Fig. 5) and two sites in Migi Sawa (G and I) on 10–12 July 1991. The sites ranged from 40 to 85 m long. We captured fish by angling in four longer reaches of the two streams during 15 June to 12 July 1991: downstream sympatric reaches in Poroshiri (D; electrofishing and cast net also used) and Migi Sawa (H), and upstream reaches where *S. malma* were allopatric in Poroshiri (A) and Migi Sawa (E and F). Charr were also captured in the most upstream (A, angling only) and downstream reaches (D) in Poroshiri during 23 June to 10 July 1992. These methods were judged sufficient to determine changes in relative abundance of the two charr species along the altitudinal gradient. Upstream boundaries of *S. leucomaenis* distribution were verified by underwater observation.

We measured the fork length (mm) of each fish captured, and for most samples determined ages using otoliths (Heiser 1966; Jearld 1983). Lengths of each age-class were compared using analysis of variance (ANOVA) based on general linear models (SAS 1992) to assess differences in growth between species and among different reaches.

Habitat measurements were made at the four sites where charr abundance was estimated by electrofishing (B, C, G, I), the same day that fish were captured. Stream width at the water surface was measured perpendicular to flow at equal intervals spaced 2.5–5.0 m apart, depending on site length. Area and maximum depth of each pool were also measured.

Population density of age-1 and older charr in individual pools of Poroshiri Stream was estimated by underwater observation during mid-June to mid-July of 1991 (n=59) and 1992 (n=56), and August 1993 (n=87). Pools in the downstream sympatric reach (D) and upstream allopatric reach (A) were observed in all 3 years. In 1993, pools in the middle sympatric reach (785–875 m) were also observed. Area and maximum depth of each pool were measured.

Results

Charr distribution across Hokkaido

When viewed at the scale of the whole island, each species of charr was distributed throughout most of Hokkaido (Fig. 1), but *S. leucomaenis* were more widely distributed to the west and south, whereas *S. malma* were distributed mostly in eastern Hokkaido and the central mountain region, and patchily elsewhere. Many river

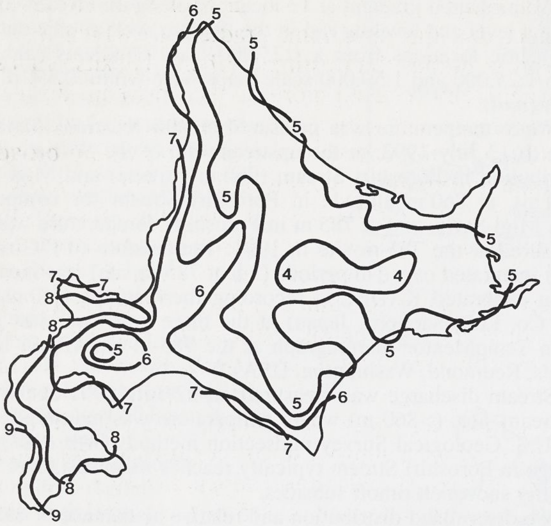

Fig. 2 Isotherms of mean annual air temperature (°C) for Hokkaido Island, based on data from 1979 to 1987 (after Anonymous 1991)

systems were inhabited by both species, but strict sympatry in streams (i.e., both species found at the same site) was relatively uncommon (26 of 360 sites; Poroshiri was an additional sympatric site).

The two charr species were also not sympatric in any Hokkaido lakes. *S. malma* are found only in two high-altitude lakes isolated by barriers to upstream dispersal, Bankei Pond (910 m altitude), 15 km north of Shikotsu Lake, and Lake Shikaribetsu (800 m) in the Hidaka Mountains (Fig. 1). The latter supports a unique subspecies adapted to the lacustrine environment called miyabe charr (*S. m. miyabei*), which has more gill rakers than any other population worldwide (Maekawa 1978, 1984). In contrast, *S. leucomaenis* were found in many low-altitude lakes, of which Akan Lake (420 m) and Okotanpe Lake (520 m; close to Shikotsu Lake) are among the highest.

The distribution of charr species across Hokkaido coincided with differences in air temperature produced by ocean currents and weather patterns (Fig. 2). Mean annual air temperatures are 2–4°C higher in Oshima Peninsula (7–9°C) than in Shiretoko Peninsula (5°C). Mean air temperatures are also 5°C or less throughout much of the Hidaka Mountains and at the highest altitudes in the Shikotsu region. As a result, the distribution of *S. malma* nearly coincided with the warmth index WI. Overall, 94% of sites with allopatric *S. malma* (n=123) were in regions where WI≤50, whereas only 38% of sites with allopatric *S. leucomaenis* were (n=211). Of sympatric sites (n=27; includes Poroshiri) 67% had WI≤50.

Longitudinal distribution within regions

In regions of Hokkaido where the two charr species co-occur, such as Shibetsu, Hidaka, and Shikotsu, their longitudinal distribution differed, with *S. malma* occupying primarily the mountain headwaters and *S. leucomaenis* extending downstream onto the plains, usually to the river mouth. Within each region, *S. malma* generally inhabited sites at higher altitude and *S. leucomaenis* those at lower altitude, with broad overlap between species (Fig. 3). However, the lower limit of the altitudinal distribution of *S. malma* and the upper limit of *S. leucomaenis* distribution generally decreased from south-west to north-east across Hokkaido, coincident with the general decrease in mean temperature (Fig. 2). The altitude range of sympatric sites also showed a similar decline in the same direction in the three central regions, despite the small sample size. The northern Hokkaido region was not included in this analysis because charr were collected at only 29 sites.

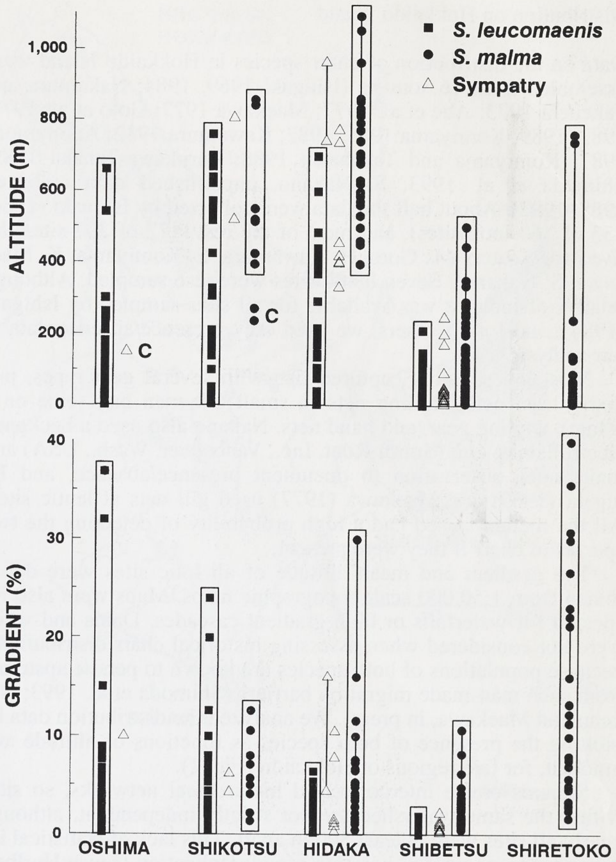

Fig. 3 Altitude (*above*) and gradient (*below*) distribution of sites with *S. leucomaenis*, *S. malma*, and both species in sympatry in five regions of Hokkaido (see Fig. 1). *Vertical lines* denote sites with altitude range >100 m in altitude. Poroshiri Stream in the Hidaka region had charr in sympatry over 730–960 m altitude and 4.4–16% gradient, and *S. malma* in allopatry over 960–1050 m altitude and 16–30% gradient. Two sites in Shikotsu and one in Oshima Peninsula were influenced by cold springs (*C, top panel*) and so were not included in *open bars* showing altitude ranges for each species

As a result of the shifts in longitudinal distribution, the two peninsulas, Shiretoko and Oshima, each had only one species. Throughout Shiretoko Peninsula, *S. malma*

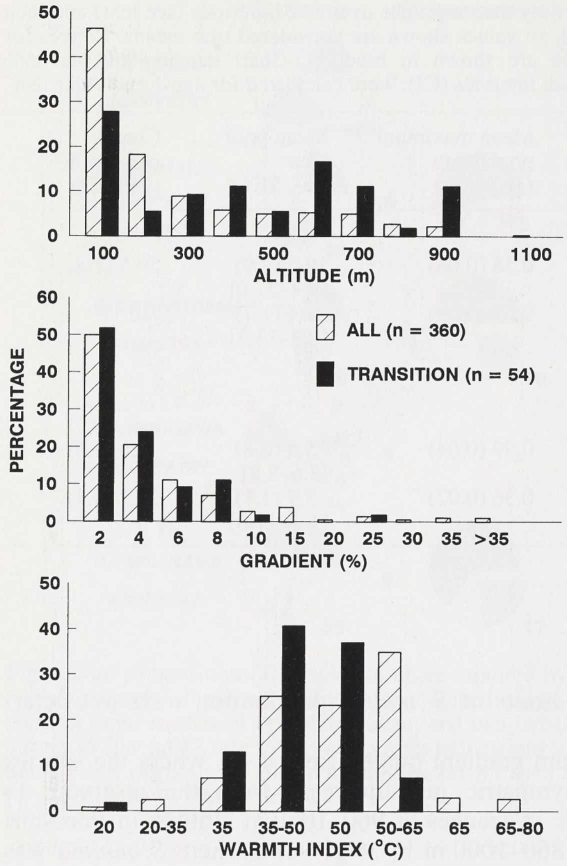

Fig. 4 Distributions of altitude (e.g., 0–100 m, etc.), gradient (e.g., 0–2%), and warmth index (WI; see text) for all 360 sites where *S. leucomaenis*, *S. malma*, or both species occurred on Hokkaido, and at transition points from *S. leucomaenis* (or sympatry) to *S. malma* along 54 individual stream courses. Sites either lay on isopleths of the WI (e.g., 50°C; see Fig. 2 in Yabe 1993) or in intervals between isopleths (e.g., 35–50°C)

occupied the entire lengths of short, steep streams that drain directly to the ocean. In contrast, in Oshima Peninsula *S. malma* occurred only in one moderate-gradient reach with many cold springs located above a high-gradient reach with cascades and small falls, whereas *S. leucomaenis* occupied many other mountain streams. Although the two species were sympatric in this Chihase River tributary (Fig. 1), *S. malma* dominated in abundance (9:1, *n*=39). Similarly, the two sites in Shikotsu where *S. malma* occurred in allopatry at the lowest altitude are also small, cold, low-gradient spring-fed streams.

Charr distributions also varied with stream gradient among the regions (Fig. 3). Although both species occupied low-gradient sites in the three central regions of Hokkaido, the highest gradient to which each extended shifted across the island. For example, *S. leucomaenis* occupied streams of more than 30% gradient in Oshima Peninsula, but lived only in streams of about 3% gradient or less in Shibetsu. In contrast, *S. malma* extended to gradients of 40% in the steep streams of Shiretoko Peninsula, but to only 10–15% in Shikotsu. However, we suspect that the maximum gradient to which *S. malma* extend is higher than estimated here, because investigators generally focused more on the upstream limit of the *S. leucomaenis* distribution than on that of *S. malma*.

Although the two charrs appear to overlap broadly in altitude and gradient within regions (Fig. 3), most overlap was due to different distributions among streams rather than sympatry in any given stream. Both altitude and gradient at transition points from *S. leucomaenis* (or sympatry) to *S. malma* differed significantly among the three central regions (Shikotsu, Hidaka, Shibetsu) where sufficient sample sizes were available for testing (Kruskal-Wallis test, $P<0.0001$ for both). These transition points generally descended to lower altitude and gradient from south-west to north-east. For Shikotsu ($n=9$), Hidaka ($n=22$), and Shibetsu ($n=20$), the median altitude of transitions was 515 m (two cold low-altitude sites deleted, Fig. 3), 591 m, and 64 m, respectively, and the median gradient was 6.6%, 2.9%, and 0.8%.

Partitioning the effects of altitude and gradient on charr distributions is difficult because the two were correlated across sites ($r=0.26$, $P<0.01$, $n=360$), and relatively few high-gradient sites occurred at low altitudes, except in the two peninsulas where the species were not sympatric. For example, there was no critical altitude or gradient associated with the transition points (Fig. 4). The ranges of these variables encompassed those for all sites and the distributions of the two samples were similar. Only three transitions might have been due to waterfalls shown on maps, where only *S. malma* was present above the falls but *S. leucomaenis* was present below. At several sites, including the one in Oshima Peninsula, the species were sympatric above falls. In contrast to altitude and gradient, the transition points did occur over a relatively narrow range of WI values (a correlate of stream temperature) when compared to all sites. Overall, 78% of transition points either lay on the 50°C isopleth of WI or in the interval between the 35 and 50°C isopleths, compared to only 49% of all sites. Moreover, five of eight transition points located on the 20°C or 35°C isopleths (seven in Hidaka, one in northern Hokkaido) were estimated from single sites with allopatric *S. malma* which had no downstream site for comparison, so it is likely that these transition points were warmer than estimated. Similarly, all four transition points in the 50–65°C interval (all in Shibetsu) were within 5 km of the 50°C isopleth.

Distribution in Poroshiri Stream

Abiotic factors

Although the distribution of charr species in Poroshiri Stream followed the same longitudinal pattern as in other Hokkaido streams, abiotic variables at the transition between sympatry and allopatry were substantially different in the main stream and its tributary. The two charr species were sympatric in downstream reaches,

Table 2 Characteristics of habitat and charr populations at four sympatric sites in Poroshiri Stream and Migi Sawa sampled by electrofishing, 10–12 July 1991, and water temperature at four locations (letters refer to sites in Fig. 5). Water temperatures were integrated by thermographs over 1–2 h periods (see text) and then averaged, so values shown are considered true means. Ranges for pool area are shown in brackets. Charr density, and its 95% confidence intervals (CI), were calculated for age-1 and older fish

Site (altitude, m)	Mean temperature (°C)	Mean width (m)	Total area (m^2)	Mean maximum pool depth (m, SE)	Mean pool area (m^2, SE)	Charr per 100 m^2 (95% CI)
Poroshiri Stream						
B. Upstream sympatry (940 m)	8.2	4.6	305	0.58 (0.06)	10.5 (2.9) [4.4–27.0]	29.5 (1.8)
C. Middle sympatry (860 m)	8.7	4.3	199	0.59 (0.05)	7.4 (1.7) [2.9–13.3]	(20.1)[a]
D. Downstream sympatry (785 m)	8.6[b]					
Migi Sawa						
G. Upstream sympatry (850 m)	7.1	2.9	117	0.39 (0.04)	5.5 (0.8) [3.6–8.8]	9.6 (4.5)
I. Downstream sympatry (780 m)	–[c]	3.4	291	0.36 (0.02)	5.7 (1.1) [1.1–11.0]	29.1 (5.4)

[a] An underestimate, because based on one electrofishing pass only
[b] Mean temperature at this site in 1991 was 8.7°C
[c] Temperature not recorded

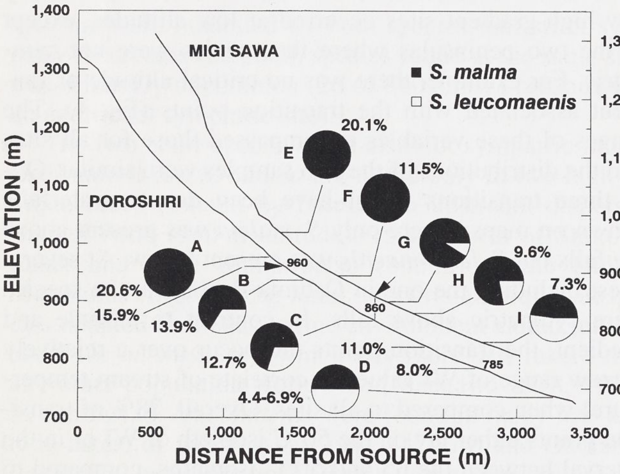

Fig. 5 Longitudinal profiles of Poroshiri Stream and Migi Sawa from headwaters downstream to a reservoir, showing relative abundance of two charr species and gradient at selected locations. The profile for Migi Sawa is offset by 50 m (refer to right ordinate) for clarity. *Arrows* indicate the upstream limit of *S. leucomaenis* distribution in each stream, and *small numbers between profiles* are altitudes for four sites where temperature and discharge were measured (see text). *Letters* refer to reaches where charr were sampled. Altitude (m) of reaches: *A* 960–1050, *B* 940, *C* 860, *D* 730–785, *E* 950–1000, *F* 870–930, *G* 850, *H* 830, *I* 780

occurring in about equal proportions by number at sites below 800 m altitude in both Poroshiri Stream and Migi Sawa (Fig. 5). The proportion of *S. leucomaenis* declined gradually upstream in both streams, but its upstream limit was at 100 m higher altitude in Poroshiri (960 m) than in Migi Sawa (860 m). There were no permanent barriers to upstream dispersal of charr to at least 1050 m in Poroshiri and 1000 m in Migi Sawa, the highest sites where *S. malma* were captured. The upstream limits of *S. malma* distribution were not determined.

Stream gradient ranged from 4.4% where the species were sympatric just upstream from the reservoir, to 20–30% in reaches at 960–1050 m altitude in Poroshiri and at 860–1000 m in Migi Sawa where *S. malma* was allopatric. The gradient was 16% at the upstream limit of *S. leucomaenis* distribution in Poroshiri, but was only about 10% at the upstream limit in Migi Sawa (Fig. 5).

Water temperature was generally lower at upstream sites of higher altitude than at those downstream, but temperatures in Migi Sawa were colder than at the same altitude in Poroshiri (Table 2). Mean temperature at the upstream limit of *S. leucomaenis* distribution in Poroshiri (960 m) was 8.2°C, 0.5°C colder than the two sites downstream (860 and 785 m) which had nearly identical temperatures. In contrast, temperature at the upstream limit of *S. leucomaenis* in Migi Sawa (860 m) averaged 7.1°C, 1.1°C colder than at the analogous point in Poroshiri (960 m) and 1.6°C colder than at the same altitude (860 m) in Poroshiri. Temperatures were nearly identical during the mid-June to mid-July study periods in 1991 and 1992 at the downstream site (785 m) in Poroshiri (Table 2).

Habitat for charr was more restricted at the upstream limit of the *S. leucomaenis* distribution in Migi Sawa than at either upstream site in Poroshiri. Stream discharge measured on 12 July 1992 was the same at the two Poroshiri sites (0.24 $m^3 \cdot s^{-1}$), but was less than half this at the upstream limit in Migi Sawa (0.11 $m^3 \cdot s^{-1}$). Discharge immediately downstream from the Migi Sawa confluence in Poroshiri (755 m) was about twice that of upstream sites (0.51 $m^3 \cdot s^{-1}$) on the same day. A severe flood apparently occurred between the two summers only in Migi Sawa, because afterwards riparian saplings were bent sharply downstream while those upslope were

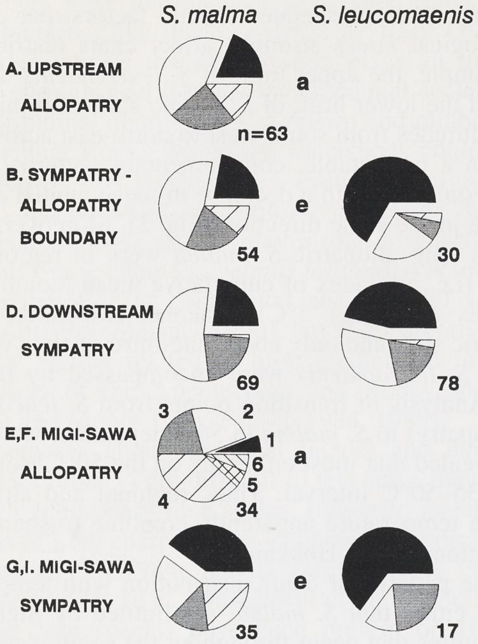

Fig. 6 Age composition of samples of charr captured by angling only (*a*), electrofishing only (*e*), or by several methods (*site D*, see text), in three reaches of Poroshiri Stream and two in Migi Sawa during 15 June to 12 July 1991 (*letters* refer to locations in Fig. 5). Sample size (*n*) is shown for each site. The *key for ages* is shown for the Migi Sawa allopatric reach

intact. In Migi Sawa the boulder-strewn floodplain averaged about 20 m wide and lacked riparian vegetation, whereas the riparian zone in Poroshiri was narrower and well vegetated with trees and shrubs.

The Migi Sawa channel was substantially narrower at both sympatric sites where charr were sampled by electrofishing than at either sympatric site in Poroshiri (Table 2), and had pools with shallower maximum depth (Wilcoxon's two-sample test, $P<0.002$). Pool area varied widely, but was not significantly different between the two streams ($P>0.10$). Habitat characteristics were similar at the two sites within each stream.

Charr populations

Density, age composition, and growth of charr also differed among sites. Total density of charr at the upstream limit of *S. leucomaenis* distribution in Migi Sawa (site G) was only about a third that at the analogous point (B) in Poroshiri ($P<0.00001$ by z-test; Table 2). Although the estimate for the 860-m site in Poroshiri (C) underestimated true charr density because it was based on only one electrofishing pass, it nevertheless was significantly greater ($P<0.00001$) than the density at the same altitude in Migi Sawa (G). Indeed, density at the most downstream site in Migi Sawa (I) was similar to the most upstream sympatric site in Poroshiri (B).

The age structure of *S. malma* populations was substantially older than *S. leucomaenis* at all sympatric sites, especially those upstream (Fig. 6; $P<0.01$ by G-test at sites B and D in Poroshiri, $P=0.24$ at sites G and I combined in Migi Sawa due to small sample size; ages 3 and 4 combined for all tests). Older *S. malma* of age 4–6 were prevalent in all except the most downstream reach of Poroshiri in 1991, whereas age-4 *S. leucomaenis* were rare or absent at all three sympatric sites where fish were aged. The same pattern held for 1992, when charr were sampled only from the most upstream and downstream reaches of Poroshiri. In that year, age-4 *S. malma* made up 44% of the sample at the upstream allopatric site (A, $n=39$) and 12% at the downstream site (D, $n=52$), but age-4 *S. leucomaenis* made up only 7% of the sample at the downstream site ($n=61$). Electrofishing provided relatively unbiased estimates of age structure, because an estimated 81–96% of the populations were captured after two passes, assuming constant capture probabilities (cf. Riley and Fausch 1992). Angling and cast-netting selected for larger fish and probably underestimated abundance of age-1 charr, but were comparable within a given reach. Despite potential biases, all samples indicated that age-1 *S. leucomaenis* were more abundant than age-1 *S. malma*. For example, in the two reaches sampled by electrofishing near the upstream end of *S. leucomaenis* distribution, age-1 *S. leucomaenis* made up 65–67% of the fish captured whereas age-1 *S. malma* made up only 22–40%.

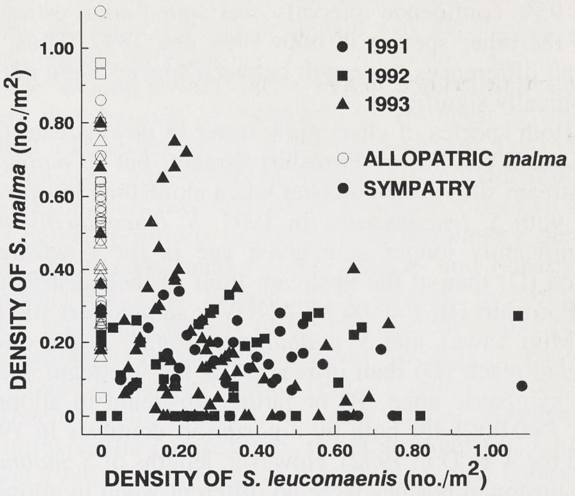

Fig. 7 Density of *S. leucomaenis* versus density of *S. malma* for individual pools in Poroshiri Stream during summers of 1991 through 1993. Density was measured by underwater observation. *Open symbols* refer to pools in the upstream reach where *S. malma* were allopatric, and *filled symbols* refer to the downstream reach where both species were sympatric

Growth of both species of charr was similar in each of the three sympatric reaches sampled. A general linear model (ANOVA) of fish length as a function of species, reach, and age showed a significant effect of species for 1991 ($P=0.02$ by ANOVA) but not for 1992 ($P=0.08$). Interactions were never significant. However, predicted mean lengths for *S. malma* and *S. leucomaenis* of ages 1–3 differed by only 1–7% in each reach in 1991, and the 95% confidence intervals overlapped point estimates for the other species in both 1991 and 1992. Thus, the small differences in growth between species were not biologically significant.

Both species of charr grew faster in downstream than upstream reaches of Poroshiri Stream, but *S. malma* at upstream sites grew no faster when alone than in sympatry with *S. leucomaenis*. In 1991, *S. leucomaenis* were significantly longer at a given age in the downstream reach (D) than at the upstream limit of their distribution in Poroshiri (B; P=0.04 by ANOVA; sample size too low in Migi Sawa), and *S. malma* were longer in the downstream reach (D) than in reaches at the upstream end of the sympatric zone (B) or farther upstream in allopatry (A; P<0.0001 for both by a posteriori contrasts in 1991, and for A vs D in 1992). However, lengths of *S. malma* in the upstream reaches were no different when in allopatry versus sympatry with *S. leucomaenis*, either in Poroshiri (A vs B; P=0.19) or Migi Sawa (E–F vs G; P=0.71).

Densities of the two charr species in individual pools throughout Poroshiri Stream were negatively correlated in each of the 3 years (Fig. 7). The relationships were strongest after logarithmic transformation of *S. leucomaenis* density for all years (1991: r= –0.76, P<0.0001, n=59; 1992: r= –0.55, P<0.0001, n=56; 1993: r= –0.56, P<0.0001, n=87). The *S. malma* were at highest density in the upstream allopatric reach, whereas *S. leucomaenis* were at highest density downstream, so total charr density in the two reaches was not significantly different in any year (Wilcoxon's two-sample test, P=0.20–0.76). Neither total density, nor that of either species, was significantly correlated with maximum pool depth, an indicator of pool size (e.g., maximum depth and area were significantly correlated in all 3 years; r=0.40–0.60; P=0.002–0.0001), except for *S. malma* density in 1992 (r= –0.38, P=0.003). However, this negative correlation was due to higher density of *S. malma* in the upstream allopatric reach, where pools were significantly shallower than downstream (Wilcoxon's two-sample test, P=0.04).

Discussion

Different abiotic and biotic factors appear important in influencing distributions of the two charr species in Hokkaido streams when viewed at different scales. Here we evaluate the most promising hypotheses about factors that affect charr distributions (Table 1), reject those that appear untenable, and explore the linkages among factors across scales. We know of few other ecological studies that have considered alternative hypotheses in this kind of analysis (Wiens 1989a; Hall et al. 1992; but see Schluter and Grant 1982; Townsend and Crowl 1991).

Abiotic factors

When viewed at spatial scales varying from the whole island to a single watershed, our data indicate that temperature and other interrelated abiotic factors that produce physiological stress strongly affect charr distributions. For example, the upper limit of *S. leucomaenis* distribution and the lower limit of *S. malma* shift from higher to lower altitudes from south-west to north-east across Hokkaido in a predictable, complementary pattern (Fig. 3), which coincides with a decrease in mean annual air temperature in the same direction (Fig. 2). Moreover, nearly all sites with allopatric *S. malma* were in regions with WI≤50 (i.e., an index of cumulative mean monthly temperatures exceeding 5°C), whereas two-thirds of the sympatric sites and only about one-third of sites with allopatric *S. leucomaenis* were encompassed by this isopleth. Analysis of transition points from *S. leucomaenis* (or sympatry) to *S. malma* in 54 independent watersheds also revealed that most either lay on the 50°C isopleth or in the 35–50°C interval. Thus, regional and altitudinal shifts in temperature apparently combine to shape charr distributions across Hokkaido.

These patterns of charr distribution with temperature suggest either that *S. malma* are limited by high water temperatures that occur throughout the south-west and at low altitudes in central regions, or that *S. leucomaenis* are limited by low temperatures in the north-east and at high altitudes in central Hokkaido, or both. The first hypothesis is further supported by the presence of *S. malma* only in cold, spring-fed streams in Oshima Peninsula and at the two lowest-altitude sites where it occurs in Shikotsu. It is perhaps not surprising that *S. malma* ascend to higher gradients in northeastern than southwestern Hokkaido (Fig. 3), and that *S. leucomaenis* show the opposite pattern, given the significant correlation between altitude and gradient. However, the patterns for altitude and gradient differ in that both species also live in low-gradient streams in all regions where the species are widely distributed, suggesting that gradient is not of primary importance in influencing charr distributions.

Despite evidence from patterns across Hokkaido that altitude and temperature are of primary importance in shaping charr distributions, data at the scale of a single watershed indicate that the relationship is imprecise and that abiotic factors may interact. *S. leucomaenis* ascended to substantially higher altitude and gradient in Poroshiri Stream than in its main tributary (Fig. 5). However, Poroshiri also had warmer summer water temperatures at a given altitude than Migi Sawa (Table 2), greater baseflow discharge, deeper pools, and a more benign flow regime, suggesting that *S. leucomaenis* may be able to ascend upstream and persist where abiotic factors and disturbance from floods are less harsh.

Altitudinal distribution patterns in other guilds of stream salmonids also suggest that the importance of temperature relative to other abiotic factors changes with scale. Fausch (1989) reported that brown trout (*Salmo trutta*), originally introduced from Europe, are distributed in North America north to the 5.5–8°C isotherms of mean annual air temperature, and that rainbow trout (*Oncorhynchus mykiss*) have become established north to the 4–7°C isotherms in the central and eastern United States where they were introduced outside their native range. These patterns, like those reported by Root (1988a, b) for birds, indicate that temperature plays an important role in shaping distributions at continental scales. However, altitudinal distributions of brown and rainbow trout in individual Rocky Mountain watersheds could not be explained by low temperatures, even after adjusting for latitude and potential competitors, suggesting that other site-specific abiotic factors play a role. Similarly, distribution of brook charr (*Salvelinus fontinalis*) is limited by high temperature at continental and regional scales in North America (Meisner 1990), but is apparently limited more by factors related to high gradient in individual watersheds of the Appalachian and Rocky mountains (Larson and Moore 1985; Fausch 1988, 1989).

Hypotheses about historical factors and barriers to dispersal (Table 1) are difficult to test since they usually involve evolutionary time scales. However, isolated populations of both charr species have distinct morphologies (Maekawa 1977, 1984; Takami and Kinoshita 1990) and isozyme profiles (e.g., Mitsuboshi et al. 1992), suggesting that both species have been present on Hokkaido long enough to disperse throughout the island, respond to abiotic factors, and interact with each other. A plausible hypothesis is that both charr species dispersed south from their centers of origin by anadromy during cooler glacial periods 10^4–10^5 years ago, but that *S. malma* shifted to fluvial life-history at the southern edge of its range in Hokkaido and retreated into colder headwaters as the climate warmed. A similar pattern of fluvial headwater populations is seen for *S. leucomaenis* near the southern edge of its range in Honshu (Kawanabe 1989).

Three factors related to abiotic features or other resources (Table 1) appear unlikely to strongly influence charr distributions in Hokkaido, although we have little direct data to evaluate their importance. Because both species use similar pool habitats (Furukawa-Tanaka 1989; Fig. 7), and feed on similar aquatic and terrestrial invertebrates (Furukawa-Tanaka 1985; Nakano and Furukawa-Tanaka 1994), the lack of suitable or sufficient habitat, or of a critical resource such as food, appear unlikely to explain why distributions of the two species are so different.

Biotic factors

Strong interspecific competition is suspected to set distribution limits in many salmonid guilds, but is easiest to detect where introduced species displace native ones (e.g., Fausch and White 1981, 1986; see review by Fausch 1988). Introduced salmonids can also limit native fishes to refuges upstream of barriers by strong predation (Townsend and Crowl 1991). However, we suspect that neither predation nor disease play strong roles in influencing Hokkaido charr distributions (Table 1) because the two species are probably susceptible to similar predators due to their similar ecology, and similar pathogens due to their close phylogenetic relationship (Cavender 1989). Thus, these factors, like habitat and other critical resources, seem unlikely to explain why the species' distributions are different.

The evidence that interspecific competition limits charr distributions in Hokkaido is strongest at scales within and among pools in Poroshiri Stream. For example, intensive underwater observation in individual pools over 4 summers revealed that individuals of the two species defend positions in interspecific dominance hierarchies (Furukawa-Tanaka 1989; Nakano and Furukawa-Tanaka 1994; K. D. Fausch and S. Nakano, unpublished data). Moreover, density of the two species among pools throughout Poroshiri Stream was strongly negatively correlated in each of 3 years (Fig. 7), indicating that interspecific competition is at least similar in intensity to intraspecific competition, if not stronger (cf. Underwood 1986). An alternative hypothesis is that major habitat differences in upstream versus downstream reaches could account for the differences in density (Wiens 1989a). However, the only significant correlation of charr density with pool size (for *S. malma* in 1992) was negative, apparently due to the prevalence of shallow pools in the upstream allopatric reach, which helps refute this alternative. Overall, such complementary density compensation is consistent with the hypothesis that interspecific competition plays a strong role at this scale (cf. Tonn 1985).

Biotic interactions such as interspecific competition, which necessarily occur as a result of interactions between individual fish, become more difficult to detect at

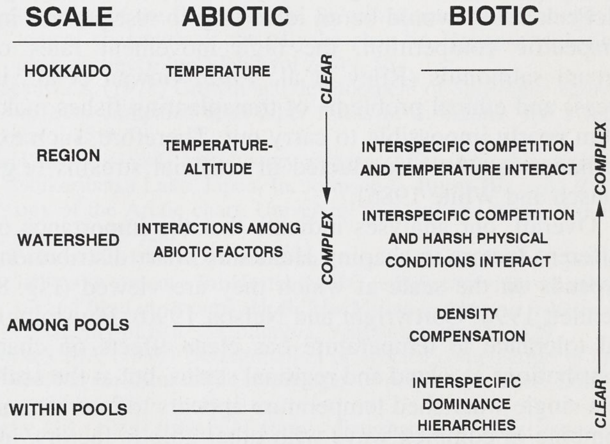

Fig. 8 A conceptual model of how the importance of various factors in influencing limits of charr distributions in Hokkaido depends on the scale at which they are analyzed. *Temperature* and *altitude* have clear effects at island and regional scales, but interact in complex ways with other abiotic factors at the scale of a single watershed. In contrast, *interspecific competition* is readily observed in individual pools of Poroshiri Stream, and *density compensation* occurs among pools, but low apparent survival of *S. leucomaenis* at its upstream limit in the Poroshiri watershed may be due to interactions between *harsh physical conditions* and *competition* with *S. malma*. Similarly, distribution patterns at the regional scale suggest that *interspecific competition* interacts with *temperature* in complex ways (see text). *Horizontal lines* indicate that abiotic and biotic factors were not considered at these scales

larger scales, and may interact with abiotic factors. It is perhaps not surprising that growth of *S. malma* was no different in allopatry versus adjacent reaches where the species were sympatric, given that charr populations are generally regulated more by mortality or emigration than growth during ages 0–2 (e.g., McFadden 1969; Saito 1975). However, age composition of the two species (Fig. 6) suggested that *S. leucomaenis* either survived poorly from age 1 to 2, relative to *S. malma*, near its upstream limit, or that juvenile *S. leucomaenis* emigrated downstream. This may be due either to competition from *S. malma*, harsh physical conditions, or both.

Analysis of niche shifts at the scale of regions, or the whole island, must necessarily assume that "all other things are equal", the *ceteris paribus* caveat of Wiens (1989a), which is unlikely to hold true at such large spatial scales because many factors combine and interact to produce the patterns observed (Hall et al. 1992). Despite this, the low incidence of sympatry (27 of 360 sites) for *S. leucomaenis* and *S. malma* in Hokkaido, though not testable using contingency analysis due to lack of statistical independence among sites, is biologically significant, in our view, because many investigators supplying data specifically searched for such locations (e.g., Ishigaki 1984). These data indicate a rather sharp boundary between species along individual stream courses (S. Nakano, personal observation), suggesting parapatric distributions and the occurrence of present or past interspecific competition. Unfortunately, hypotheses about interspecific competition operating in the past (i.e., "the ghost"; Connell 1980) are not amenable to direct testing (Wiens 1989a). Although transplant experiments (e.g., McPeek 1990) would be an ideal way to test present interspecific competition, the high movement rates of stream salmonids (Riley et al. 1992; Gowan et al., in press) and ethical problems of transplanting fishes make them nearly impossible to carry out. Therefore, such experiments are best conducted in artificial streams (e.g., Fausch and White 1986).

Overall, our analyses indicate that the importance of different factors in shaping Hokkaido charr distributions depends on the scale at which they are viewed (Fig. 8; Bennett 1990; Cortwright and Nelson 1990). Physiological tolerance to temperature has clear effects on charr distributions at island and regional scales, but at the scale of a single watershed temperature appears to interact and combine in complex ways with other abiotic factors, including disturbance from floods (cf. Meffe 1984; Bramblett and Fausch 1991). In contrast, interspecific competition can be directly observed in individual pools of Poroshiri Stream, and plays a strong role in regulating density among pools, but detecting it at larger scales is complicated by interactions with abiotic factors. For example, one hypothesis is that *S. malma* are limited downstream primarily by a suite of abiotic factors related to temperature, whereas *S. leucomaenis* are limited upstream by interactions between harsh physicochemical conditions and interspecific competition with *S. malma*. An alternative is that competitive superiority shifts from *S. leucomaenis* to *S. malma* as temperature decreases upstream (Dunson and Travis 1991; De Staso and Rahel 1994). A clearer understanding of how interactions between temperature and interspecific competition influence distributions of charr species in Hokkaido must await tests of critical hypotheses such as these, via field and laboratory experiments.

Acknowledgements Koji Maekawa and Akira Goto provided data and information about charr distributions in several Hokkaido regions. Satoshi Kitano provided able field assistance for work in Poroshiri Stream, and Yoshinori Taniguchi measured stream characteristics from maps. We thank Hiroya Kawanabe for advice and administration of research funding. Robert Behnke, Kevin Bestgen, Charles Gowan, Frank Rahel, John Wiens, and an anonymous reviewer gave constructive criticism on earlier manuscript drafts. This research was jointly funded by the National Science Foundation (grant INT-9016512 from the International and Ecology Programs to K. D. Fausch) and the Japan Society for the Promotion of Science (grant to Hiroya Kawanabe, Makoto Nagoshi, Koji Maekawa, Shigeru Nakano, Teruaki Hino, and Katsuki Nakai) under the U. S.-Japan Cooperative Science Program.

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Enjoy

Nonoverlapping Magisteria

Science and religion are not in conflict, for their teachings occupy distinctly different domains.

By Stephen Jay Gould

Joan Hall

Incongruous places often inspire anomalous stories. In early 1984, I spent several nights at the Vatican housed in a hotel built for itinerant priests. While pondering over such puzzling issues as the intended function of the bidets in each bathroom, and hungering for something other than plum jam on my breakfast rolls (why did the basket only contain hundreds of identical plum packets and not a one of, say, strawberry?), I encountered yet another among the innumerable issues of contrasting cultures that can make life so interesting. Our crowd (present in Rome for a meeting on nuclear winter sponsored by the Pontifical Academy of Sciences) shared the hotel with a group of French and Italian Jesuit priests who were also professional scientists.

At lunch, the priests called me over to their table to pose a problem that had been troubling them. What, they wanted to know, was going on in America with all this talk about "scientific creationism"? One asked me: "Is evolution really in some kind of trouble; and if so, what could such trouble be? I have always been taught that no doctrinal conflict exists between evolution and Catholic faith, and the evidence for evolution seems both entirely satisfactory and utterly overwhelming. Have I missed something?"

A lively pastiche of French, Italian, and English conversation then ensued for half an hour or so, but the priests all seemed reassured by my general answer: Evolution has encountered no intellectual trouble; no new arguments have been offered. Creationism is a homegrown phenomenon of American sociocultural history—a splinter movement (unfortunately rather more of a beam these days) of Protestant fundamentalists who believe that every word of the Bible must be literally true, whatever such a claim might mean. We all left satisfied, but I certainly felt bemused by the anomaly of my role as a Jewish agnostic, trying to reassure a group of Catholic priests that evolution remained both true and entirely consistent with religious belief.

Another story in the same mold: I am often asked whether I ever encounter creationism as a live issue among my Harvard undergraduate students. I reply that only once, in nearly thirty years of teaching, did I experience such an incident. A very sincere and serious freshman student came to my office hours with the following question that had clearly been troubling him deeply: "I am a devout Christian and have never had any reason to doubt evolution, an idea that seems both exciting and particularly well documented. But my roommate, a proselytizing Evangelical, has been insisting with enormous vigor that I cannot be both a real Christian and an evolutionist. So tell me, can a person believe both in God and evolution?" Again, I gulped hard, did my intellectual duty, and reassured him that evolution was both true and entirely compatible with Christian belief—a position I hold sincerely, but still an odd situation for a Jewish agnostic.

These two stories illustrate a cardinal point, frequently unrecognized but absolutely central to any understanding of the status and impact of the politically potent, fundamentalist doctrine known by its self-proclaimed oxymoron as "scientific creationism"—the claim that the Bible is literally true, that all organisms were created during six days of twenty-four hours, that the earth is only a few thousand years old, and that evolution must therefore be false. Creationism does not pit science against religion (as my opening stories indicate), for no such conflict exists. Creationism does not raise any unsettled intellectual issues about the nature of biology or the history of life. Creationism is a local and parochial movement, powerful only in the United States among Western nations, and prevalent only among the few sectors of American Protestantism that choose to read the Bible as an inerrant document, literally true in every jot and tittle.

I do not doubt that one could find an


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occasional nun who would prefer to teach creationism in her parochial school biology class, or an occasional orthodox rabbi who does the same in his yeshiva, but creationism based on biblical literalism makes little sense in either Catholicism or Judaism, for neither religion maintains any extensive tradition for reading the Bible as literal truth rather than illuminating literature, based partly on metaphor and allegory (essential components of all good writing) and demanding interpretation for proper understanding. Most Protestant groups, of course, take the same position—the fundamentalist fringe notwithstanding.

The position that I have just outlined by personal stories and general statements represents the standard attitude of all major Western religions (and of Western science) today. (I cannot, through ignorance, speak of Eastern religions, although I suspect that the same position would prevail in most cases.) The lack of conflict between science and religion arises from a lack of overlap between their respective domains of professional expertise—science in the empirical constitution of the universe, and religion in the search for proper ethical values and the spiritual meaning of our lives. The attainment of wisdom in a full life requires extensive attention to both domains—for a great book tells us that the truth can make us free and that we will live in optimal harmony with our fellows when we learn to do justly, love mercy, and walk humbly.

In the context of this standard position, I was enormously puzzled by a statement issued by Pope John Paul II on October 22, 1996, to the Pontifical Academy of Sciences, the same body that had sponsored my earlier trip to the Vatican. In this document, entitled "Truth Cannot Contradict Truth," the pope defended both the evidence for evolution and the consistency of the theory with Catholic religious doctrine. Newspapers throughout the world responded with front-page headlines, as in the *New York Times* for October 25: "Pope Bolsters Church's Support for Scientific View of Evolution."

Now I know about "slow news days," and I do admit that nothing else was strongly competing for headlines at that particular moment. (The *Times* could muster nothing more exciting for a lead story than Ross Perot's refusal to take Bob Dole's advice and quit the presidential race.) Still, I couldn't help feeling immensely puzzled by all the attention paid to the pope's statement (while being wryly pleased, of course, for we need all the good press we can get, especially from respected outside sources). The Catholic Church had never opposed evolution and had no reason to do so. Why had the pope issued such a statement at all? And why had the press responded with an orgy of worldwide, front-page coverage?

In his 1996 statement, John Paul II defends both the evidence for evolution and the theory's consistency with Catholic teachings.

I could only conclude at first, and wrongly as I soon learned, that journalists throughout the world must deeply misunderstand the relationship between science and religion, and must therefore be elevating a minor papal comment to unwarranted notice. Perhaps most people really do think that a war exists between science and religion, and that (to cite a particularly newsworthy case) evolution must be intrinsically opposed to Christianity. In such a context, a papal admission of evolution's legitimate status might be regarded as major news indeed—a sort of modern equivalent for a story that never happened, but would have made the biggest journalistic splash of 1640: Pope Urban VIII releases his most famous prisoner from house arrest and humbly apologizes, "Sorry, Signor Galileo . . . the sun, er, is central."

But I then discovered that the prominent coverage of papal satisfaction with evolution had not been an error of non-Catholic Anglophone journalists. The Vatican itself had issued the statement as a major news release. And Italian newspapers had featured, if anything, even bigger headlines and longer stories. The conservative *Il Giornale,* for example, shouted from its masthead: "Pope Says We May Descend from Monkeys."

Clearly, I was out to lunch. Something novel or surprising must lurk within the papal statement, but what could it be?—especially given the accuracy of my primary impression (as I later verified) that the Catholic Church values scientific study, views science as no threat to religion in general or Catholic doctrine in particular, and has long accepted both the legitimacy of evolution as a field of study and the potential harmony of evolutionary conclusions with Catholic faith.

As a former constituent of Tip O'Neill's, I certainly know that "all politics is local"—and that the Vatican undoubtedly has its own internal reasons, quite opaque to me, for announcing papal support of evolution in a major statement. Still, I knew that I was missing some important key, and I felt frustrated. I then remembered the primary rule of intellectual life: when puzzled, it never hurts to read the primary documents—a rather simple and self-evident principle that has, nonetheless, completely disappeared from large sectors of the American experience.

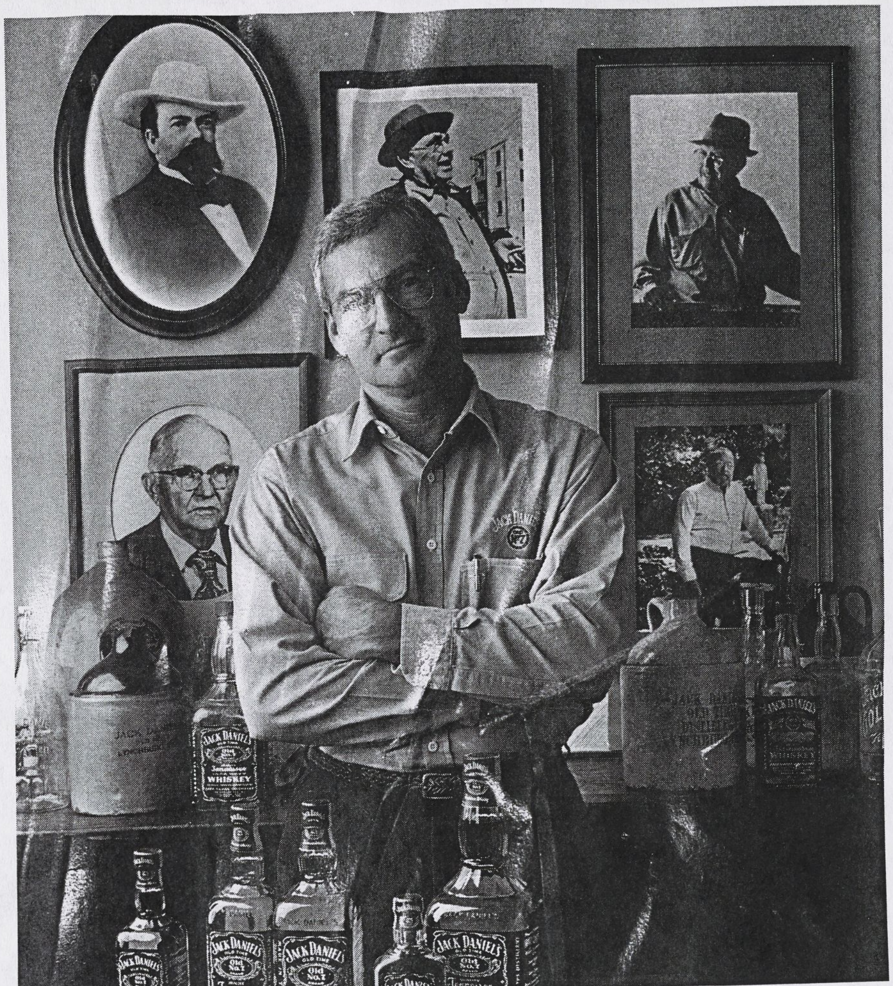
I knew that Pope Pius XII (not one of my favorite figures in twentieth-century history, to say the least) had made the primary statement in a 1950 encyclical entitled *Humani Generis.* I knew the main thrust of his message: Catholics could believe whatever science determined about the evolution of the human body, so long as they accepted that, at some time of his choosing, God had infused the soul into such a creature. I also knew that I had no problem with this statement, for whatever my private beliefs about souls, science cannot touch

3

such a subject and therefore cannot be threatened by any theological position on such a legitimately and intrinsically religious issue. Pope Pius XII, in other words, had properly acknowledged and respected the separate domains of science and theology. Thus, I found myself in total agreement with *Humani Generis*—but I had never read the document in full (not much of an impediment to stating an opinion these days).

I quickly got the relevant writings from, of all places, the Internet. (The pope is prominently on-line, but a Luddite like me is not. So I got a computer-literate associate to dredge up the documents. I do love the fracture of stereotypes implied by finding religion so hep and a scientist so square.) Having now read in full both Pope Pius's *Humani Generis* of 1950 and Pope John Paul's proclamation of October 1996, I finally understand why the recent statement seems so new, revealing, and worthy of all those headlines. And the message could not be more welcome for evolutionists and friends of both science and religion.

The text of *Humani Generis* focuses n the magisterium (or teaching author) of the Church—a word derived not from any concept of majesty or awe but from the different notion of teaching, for *magister* is Latin for "teacher." We may, I think, adopt this word and concept to express the central point of this essay and the principled resolution of supposed "conflict" or "warfare" between science and religion. No such conflict should exist because each subject has a legitimate magisterium, or domain of teaching authority—and these magisteria do not overlap (the principle that I would like to designate as NOMA, or "nonoverlapping magisteria"). The net of science covers the empirical universe: what is it made of (fact) and why does it work this way (theory). The net of religion extends over questions of moral meaning and value. These two magisteria do not overlap, nor do they encompass all inquiry (consider, for




starters, the magisterium of art and the meaning of beauty). To cite the arch clichés, we get the age of rocks, and religion retains the rock of ages; we study how the heavens go, and they determine how to go to heaven.

The Catholic Church had never opposed evolution. Why had the pope issued such a statement at all?

This resolution might remain all neat and clean if the nonoverlapping magisteria (NOMA) of science and religion were separated by an extensive no man's land. But, in fact, the two magisteria bump right up against each other, interdigitating in wondrously complex ways along their joint border. Many of our deepest questions call upon aspects of both for different parts of a full answer—and the sorting of legitimate domains can become quite complex and difficult. To cite just two broad questions involving both evolutionary facts and moral arguments: Since evolution made us th only earthly creatures with advance consciousness, what responsibilities so entailed for our relations with other species? What do our genealogical ties with other organisms imply about the meaning of human life?

Pius XII's *Humani Generis* is a highly traditionalist document by a deeply conservative man forced to face all the "isms" and cynicisms that rode the wake of World War II and informed the struggle to rebuild human decency from the ashes of the Holocaust. The encyclical, subtitled "Concerning some false opinions which threaten to undermine the foundations of Catholic doctrine," begins with a statement of embattlement:

> *Disagreement and error among men on moral and religious matters have always been a cause of profound sorrow to all good men, but above all to the true and loyal sons of the Church, especially today,*

5

> *when we see the principles of Christian culture being attacked on all sides.*

Pius lashes out, in turn, at various external enemies of the Church: pantheism, existentialism, dialectical materialism, historicism, and of course and preeminently, communism. He then notes with sadness that some well-meaning folks within the Church have fallen into a dangerous relativism—"a theological pacifism and egalitarianism, in which all points of view become equally valid"—in order to include people of wavering faith who yearn for the embrace of Christian religion but do not wish to accept the particularly Catholic magisterium.

What is this world coming to when these noxious novelties can so discombobulate a revealed and established order? Speaking as a conservative's conservative, Pius laments:

> *Novelties of this kind have already borne their deadly fruit in almost all branches of theology. . . . Some question whether angels are personal beings, and whether matter and spirit differ essentially. . . . Some even say that the doctrine of Transubstantiation, based on an antiquated philosophic notion of substance, should be so modified that the Real Presence of Christ in the Holy Eucharist be reduced to a kind of symbolism.*

Pius first mentions evolution to decry a misuse by overextension often promulgated by zealous supporters of the anathematized "isms":

> *Some imprudently and indiscreetly hold that evolution . . . explains the origin of all things . . . . Communists gladly subscribe to this opinion so that, when the souls of men have been deprived of every idea of a personal God, they may the more efficaciously defend and propagate their dialectical materialism.*

Pius's major statement on evolution

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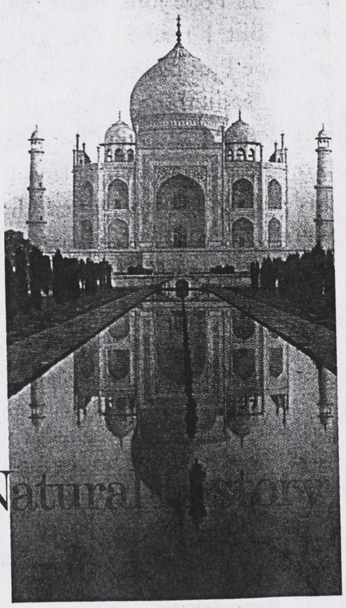

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occurs near the end of the encyclical in paragraphs 35 through 37. He accepts the standard model of NOMA and begins by acknowledging that evolution lies in a difficult area where the domains press hard against each other. "It remains for US now to speak about those questions which, although they pertain to the positive sciences, are nevertheless more or less connected with the truths of the Christian faith."*

Pius then writes the well-known words that permit Catholics to entertain the evolution of the human body (a factual issue under the magisterium of science), so long as they accept the divine Creation and infusion of the soul (a theological notion under the magisterium of religion).

> *The Teaching Authority of the Church does not forbid that, in conformity with the present state of human sciences and sacred theology, research and discussions, on the part of men experienced in both fields, take place with regard to the doctrine of evolution, in as far as it inquires into the origin of the human body as coming from pre-existent and living matter—for the Catholic faith obliges us to hold that souls are immediately created by God.*

I had, up to here, found nothing surprising in *Humani Generis,* and nothing to relieve my puzzlement about the novelty of Pope John Paul's recent statement. But I read further and realized that Pope Pius had said more about evolution, something I had never seen quoted, and that made John Paul's statement most interesting indeed. In short, Pius forcefully proclaimed that while evolution may be legitimate in principle, the theory, in fact, had not been proven and might well be entirely wrong. One gets the strong impression, moreover, that Pius was rooting pretty hard for a verdict of falsity.

In 1950, Pius forcefully proclaimed that while evolution may be legitimate, the theory had not been entirely proven. One gets the strong impression that he was rooting pretty hard for a verdict of falsity.

Continuing directly from the last quotation, Pius advises us about the proper study of evolution:

> *However, this must be done in such a way that the reasons for both opinions, that is, those favorable and those unfavorable to evolution, be weighed and judged with the necessary seriousness, moderation and measure. . . . Some, however, rashly transgress this liberty of discussion, when they act as if the origin of the human body from pre-existing and living matter were already completely certain and proved by the facts which have been discovered up to now and by reasoning on those facts, and as if there were nothing in the sources of divine revelation which demands the greatest moderation and caution in this question.*

To summarize, Pius generally accepts the NOMA principle of nonoverlapping magisteria in permitting Catholics to entertain the hypothesis of evolution for the human body so long as they accept the divine infusion of the soul. But he then offers some (holy) fatherly advice to scientists about the status of evolution as a scientific concept: the idea is not yet proven, and you all need to be especially cautious because evolution raises many troubling issues right on the border of my magisterium. One may read this second theme in two different ways: either as a gratuitous incursion into a different magisterium or as a helpful perspective from an intelligent and concerned outsider. As a man of good will, and in the interest of conciliation, I am happy to embrace the latter reading.

In any case, this rarely quoted second claim (that evolution remains both unproven and a bit dangerous)—and not the familiar first argument for the NOMA principle (that Catholics may accept the evolution of the body so long as they embrace the creation of the soul)—defines the novelty and the interest of John Paul's recent statement.

John Paul begins by summarizing Pius's older encyclical of 1950, and particularly by reaffirming the NOMA principle—nothing new here, and no cause for extended publicity:

> *In his encyclical "Humani Generis" (1950), my predecessor Pius XII had already stated that there was no opposition between evolution and the doctrine of the faith about man and his vocation.*

To emphasize the power of NOMA, John Paul poses a potential problem and a sound resolution: How can we reconcile science's claim for physical continuity in human evolution with Catholicism's insistence that the soul must enter at a moment of divine infusion:

(Please turn to page 60)

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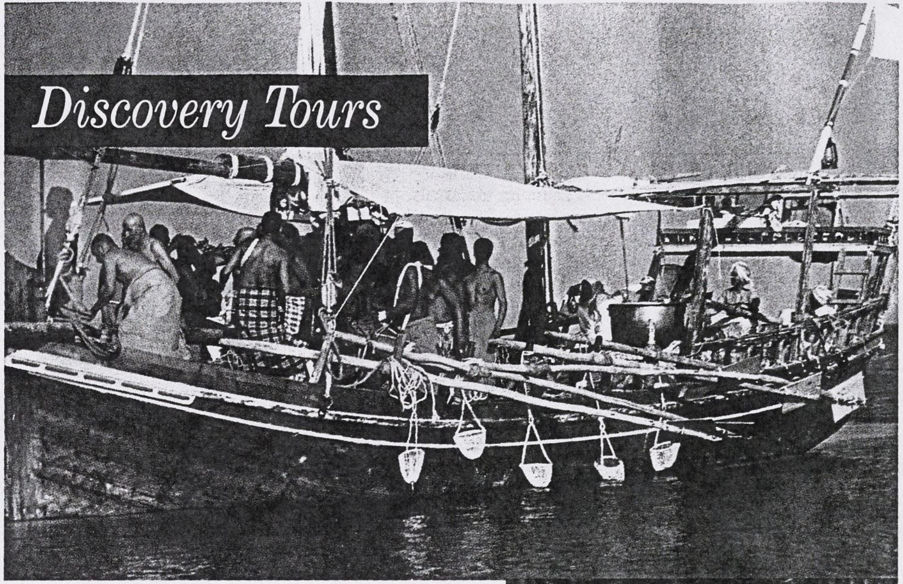
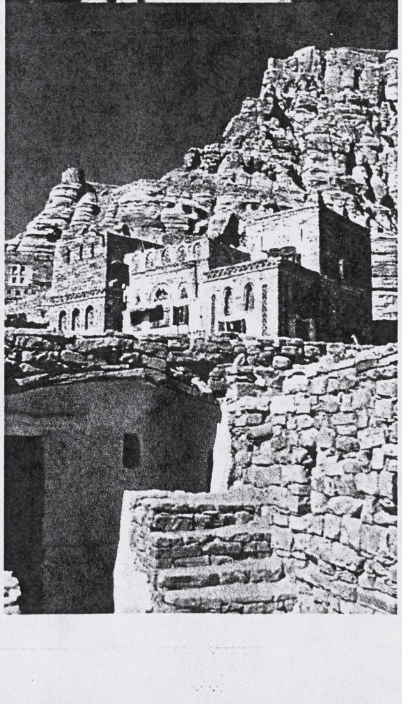
* Interestingly, the main thrust of these paragraphs does not address evolution in general but lies in refuting a doctrine that Pius calls "polygenism," or the notion of human ancestry from multiple parents—for he regards such an idea as incompatible with the doctrine of original sin, "which proceeds from a sin actually committed by an individual Adam and which, through generation, is passed on to all and is in everyone as his own." In this one instance, Pius may be transgressing the NOMA principle—but I cannot judge, for I do not understand the details of Catholic theology and therefore do not know how symbolically such a statement may be read. If Pius is arguing that we cannot entertain a theory about derivation of all modern humans from an ancestral population rather than through an ancestral individual (a potential fact) because such an idea would question the doctrine or original sin (a theological construct), then I would declare him out of line for letting the magisterium of religion dictate a conclusion within the magisterium of science.





(Continued from page 22)

> *With man, then, we find ourselves in the presence of an ontological difference, an ontological leap, one could say. However, does not the posing of such ontological discontinuity run counter to that physical continuity which seems to be the main thread of research into evolution in the field of physics and chemistry? Consideration of the method used in the various branches of knowledge makes it possible to reconcile two points of view which would seem irreconcilable. The sciences of observation describe and measure the multiple manifestations of life with increasing precision and correlate them with the time line. The moment of transition to the spiritual cannot be the object of this kind of observation.*

The novelty and news value of John Paul's statement lies, rather, in his profound revision of Pius's second and rarely quoted claim that evolution, while conceivable in principle and reconcilable with religion, can cite little persuasive evidence, and may well be false. John Paul states—and I can only say amen, and thanks for noticing—that the half century between Pius's surveying the ruins of World War II and his own pontificate heralding the dawn of a new millennium has witnessed such a growth of data, and such a refinement of theory, that evolution can no longer be doubted by people of good will:

> *Pius XII added . . . that this opinion [evolution] should not be adopted as though it were a certain, proven doctrine. . . . Today, almost half a century after the publication of the encyclical, new knowledge has led to the recognition of more than one hypothesis in the theory of evolution. It is indeed remarkable that this theory has been progressively accepted by researchers, following a series of discoveries in various fields of knowledge. The convergence, neither sought nor fabricated, of the results of work that was conducted independently is in itself a significant argument in favor of the theory.*

8

In conclusion, Pius had grudgingly admitted evolution as a legitimate hypothesis that he regarded as only tentatively supported and potentially (as I suspect he hoped) untrue. John Paul, nearly fifty years later, reaffirms the legitimacy of evolution under the NOMA principle—no news here—but then adds that additional data and theory have placed the factuality of evolution beyond reasonable doubt. Sincere Christians must now accept evolution not merely as a plausible possibility but also as an effectively proven fact. In other words, official Catholic opinion on evolution has moved from "say it ain't so, but we can deal with it if we have to" (Pius's grudging view of 1950) to John Paul's entirely welcoming "it has been proven true; we always celebrate nature's factuality, and we look forward to interesting discussions of theological implications." I happily endorse this turn of events as gospel—literally *good news.* I may represent the magisterium of science, but I welcome the support of a primary leader from the other major magisterium of our complex lives. And I recall the wisdom of King Solomon: "As cold waters to a thirsty soul, so is good news from a far country" (Prov. 25:25).

> The net of science covers the empirical universe: what is it made of (fact) and why does it work this way (theory). The net of religion extends over questions of moral meaning and value.

Just as religion must bear the cross of its hard-liners, I have some scientific colleagues, including a few prominent enough to wield influence by their writings, who view this rapprochement of the separate magisteria with dismay. To colleagues like me—agnostic scientists who welcome and celebrate the rapprochement, especially the pope's latest statement —they say: "C'mon, be honest; you know that religion is addlepated, superstitious, old-fashioned b.s.; you're only making those welcoming noises because religion is so powerful, and we need to be diplomatic in order to assure public support and funding for science." I do not think that this attitude is common among scientists, but such a position fills me with dismay—and I therefore end this essay with a personal statement about religion, as a testimony to what I regard as a virtual consensus among thoughtful scientists (who support the NOMA principle as firmly as the pope does).

I am not, personally, a believer or a religious man in any sense of institutional commitment or practice. But I have enormous respect for religion, and the subject has always fascinated me, beyond almost all others (with a few exceptions, like evolution, paleontology, and baseball). Much of this fascination lies in the historical paradox that throughout Western history organized religion has fostered both the most unspeakable horrors and the most heartrending examples of human goodness in the face of personal danger. (The evil, I believe, lies in the occasional confluence of religion with secular power. The Catholic Church has sponsored its share of horrors, from Inquisitions to liquidations—but only because this institution held such secular power during so much of Western history. When my folks held similar power more briefly in Old Testament times, they committed just as many atrocities with many of the same rationales.)

I believe, with all my heart, in a respectful, even loving concordat between our magisteria—the NOMA solution. NOMA represents a principled position on moral and intellectual grounds, not a mere diplomatic stance. NOMA also cuts both ways. If religion can no longer dictate the nature of factual conclusions properly under the magisterium of science, then scientists cannot claim higher insight into moral truth from any superior knowledge of the world's empirical constitution. This mutual humility has important practical consequences in a world of such diverse passions.

Religion is too important to too many people for any dismissal or denigration of the comfort still sought by many folks from theology. I may, for example, privately suspect that papal insistence on divine infusion of the soul represents a sop to our fears, a device for maintaining a belief in human superiority within an evolutionary world offering no privileged position to any creature. But I also know that souls represent a subject outside the magisterium of science. My world cannot prove or disprove such a notion, and the concept of souls cannot threaten or impact my domain. Moreover, while I cannot personally accept the Catholic view of souls, I surely honor the metaphorical value of such a concept both for grounding moral discussion and for expressing what we most value about human potentiality: our decency, care, and all the ethical and intellectual struggles that the evolution of consciousness imposed upon us.

If religion can no longer dictate the nature of factual conclusions, then scientists cannot claim moral truth from any superior knowledge of the world's constitution.

As a moral position (and therefore not as a deduction from my knowledge of nature's factuality), I prefer the "cold bath" theory that nature can be truly "cruel" and "indifferent"—in the utterly inappropriate terms of our ethical discourse—because nature was not constructed as our eventual abode, didn't know we were coming (we are, after all, interlopers of the latest geological microsecond), and doesn't give a damn about us (speaking metaphorically). I regard such a position as liberating, not depressing, because we then become free to conduct moral discourse—and nothing could be more important—in our own terms, spared from the delusion that we might read moral truth passively from nature's factuality.

But I recognize that such a position frightens many people, and that a more spiritual view of nature retains broad appeal (acknowledging the factuality of evolution and other phenomena, but still seeking some intrinsic meaning in human terms, and from the magisterium of religion). I do appreciate, for example, the struggles of a man who wrote to the *New York Times* on November 3, 1996, to state both his pain and his endorsement of John Paul's statement:

> *Pope John Paul II's acceptance of evolution touches the doubt in my heart. The problem of pain and suffering in a world created by a God who is all love and light is hard enough to bear, even if one is a creationist. But at least a creationist can say that the original creation, coming from the hand of God was good, harmonious, innocent and gentle. What can one say about evolution, even a spiritual theory of evolution? Pain and suffering, mindless cruelty and terror are its means of creation. Evolution's engine is the grinding of predatory teeth upon the screaming, living flesh and bones of prey. . . . If evolution be true, my faith has rougher seas to sail.*

I don't agree with this man, but we could have a wonderful argument. I would push the "cold bath" theory; he would (presumably) advocate the theme of inherent spiritual meaning in nature, however opaque the signal. But we would both be enlightened and filled with better understanding of these deep and ultimately unanswerable issues. Here, I believe, lies the greatest strength and necessity of NOMA, the nonoverlapping magisteria of science and religion. NOMA permits—indeed enjoins—the prospect of respectful discourse, of constant input from both magisteria toward the common goal of wisdom. If human beings are anything special, we are the creatures that must ponder and talk. Pope John Paul II would surely point out to me that his magisterium has always recognized this distinction, for *in principio erat verbum*—"In the beginning was the Word."

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Postscript

Carl Sagan organized and attended the Vatican meeting that introduces this essay; he also shared my concern for fruitful cooperation between the different but vital realms of science and religion. Carl was also one of my dearest friends. I learned of his untimely death on the same day that I read the proofs for this essay. I could only recall Nehru's observations on Gandhi's death—that the light had gone out, and darkness reigned everywhere. But I then contemplated what Carl had done in his short sixty-two years and remembered John Dryden's ode for Henry Purcell, a great musician who died even younger: "He long ere this had tuned the jarring spheres, and left no hell below."

The days I spent with Carl in Rome were the best of our friendship. We delighted in walking around the Eternal City, feasting on its history and architecture—and its food! Carl took special delight in the anonymity that he still enjoyed in a nation that had not yet aired Cosmos*, the greatest media work in popular science of all time.*

I dedicate this essay to his memory. Carl also shared my personal suspicion about the nonexistence of souls—but I cannot think of a better reason for hoping we are wrong than the prospect of spending eternity roaming the cosmos in friendship and conversation with this wonderful soul.

p. 119
Thaumatinus
[No date]

THE SYSTEMATIC POSITION OF PITON'S PRESUMED CHARACID FISHES FROM THE EOCENE OF CENTRAL FRANCE

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INTRODUCTION

The large and varied family of fresh-water teleostean fishes known as Characidae forms the most generalized of the living groups of the order Ostariophysi. The order is one of the largest among teleostean fishes, and, except for a few families of catfishes, is strictly confined to fresh water. The family Characidae inhabits tropical America and Africa, and probably has done so for a long time (Myers, 1938). Confinement of the characids to these southern continents, and their absence in the northern ones, is the most important of the evidence adduced by Eigenmann (1909) and Regan (1922) for the existence of a Mesozoic or early Cenozoic continental connection between Africa and South America - a subject that again is receiving attention (Mayr, 1952; Darlington, 1957). Fossil evidence of the presence of the Characidae in the northern continents would be of the utmost importance in explaining the present disjunct distribution of the members of this family. Piton's report in 1938 of two genera and two species of Characidae from the Lutetian of Puy-de-Dôme, France, apparently proved that this family existed in Europe in the early Cenozoic. In the present paper I have attempted to evaluate Piton's data and conclusions, and to make a more secure identification of the family to which his presumed characids belong.

THE CHARACIDAE

Before proceeding to a consideration of the French fossils, it seems desirable to provide some background material on the Characidae and the fossils so far referred to the family.

The order Ostariophysi is characterized by the modification of the anterior vertebrae into a *pars sustentaculum* and its associated ossicles which are together known as the Weberian apparatus (Sagemehl, 1885; Bridge and Haddon, 1893; Chranilov, 1929; Watson, 1939; Nelson, 1949; Weitzman, 1954; and others). The Weberian apparatus distinguishes these fishes from all other orders of primitive teleosts.

As noted above, the Characidae are structurally the most generalized of the Ostariophysi. Regan (1911) divided the Characidae into several families, but my own work (Weitzman, 1960a; 1960b) indicates that, for the present, Regan's families should not be recognized.

Darlington (1957) discussed the problem of how the disjunct distribution of the characids came about, and concluded that the Characidae reached South America sometime during the Cretaceous, either from Africa by a land bridge, or from tropical Asia across the Bering Land Bridge by way of North America. He also postulated that characids once existed in tropical Asia, and that there well may have been a characid fauna common to Asia and Africa. Darlington favored the hypothesis that characids reached South America from Asia by way of North America, and later became extinct in North America and Asia. Since no fossil characids are known from Asia, and the North American records of fossil characids are very dubious, this hypothesis suffers from lack of evidence. However, the fossil fishes of Asia are little known, and it is quite possible that fossil characids may

be found there. Piton's record of Eocene fossil characids from France has given support to the idea that characids have existed in Holarctica. As will be shown below, I do not believe that Piton's fossil fishes are characids, or even members of the order Ostariophysi. Thus the slim leg of support for Holarctic occurrence of characids is removed. The hypotheses of continental drift and of a Mesozoic connection between Africa and South America are not dead - even among geophysicists (Runcorn, 1959) using geophysical evidence. I believe, therefore, that the concept of characids crossing a filter land bridge between Africa and South America should receive at least as serious consideration as the concept of their migration across Asia and North America to reach South America.

Fossil characids are few in number, and so far have helped little to solve the problems of characid distribution. The best known are those from an apparently Late Tertiary lignite at Tremembé, near Taubaté, in the state of São Paulo, Brazil. Fishes from this deposit were first described by Woodward (1898), and discussed later by Eigenmann and Myers (1929), and by Schaeffer (1947), who reduced the known forms to a single genus. Recently, Travassos and da Silva Santos (1955), with more knowledge of characids and abundant material, have shown that four Recent genera are represented by fossil species at Tremembe. These are unquestionably characid fossils.

Cockerell (1921) described fish scales from a Miocene deposit in Peru which he referred to a new genus (*Characilepis*) of the Characidae, and other scales (*Erythrinolepis*) from North American Cretaceous marine deposits on which he based a new but presumably related family (Cockerell, 1919). There is no real evidence that the scales of *Erythrinolepis* are those of characids or characid-like fishes. Hay (1929, p. 719) referred the Upper Cretaceous fish genus *Ischyriza* Leidy, from the eastern and southeastern United States, to the Characidae, but no recent work has confirmed his transfer of this genus from the Esocidae, where it was formerly placed (Hay, 1902, p. 398). Leidy's specimens were teeth, and the evidence used to place them in the Characidae is of doubtful value. Other than the referral of fragments from Tertiary deposits in Peru to the Recent genus *Myletes* (Peyer, 1929), of African material to the Recent genus *Alestes* (mentioned by Romer, 1945, p. 583), and of African Pleistocene fish teeth to the genus *Hydrocyon*[1] by Greenwood (1959), this completes the records of real and presumed fossil Characidae.

THE FOSSIL FISHES OF THE MENAT SCHISTS

A schist said to be of Lutetian age, at Menat, Puy-de-Dôme, in central France, has produced several fresh-water fishes. However, the most arresting of the discoveries in this lake deposit was announced by Piton in 1938, when he described from it two new genera and two new species of presumed Characidae, *Prohydrocyon pellegrini* and *Procharacinus arverniensis*.

The schist of Menat (dated as Lutetian) is roughly equivalent in age to the Bridger (Middle Eocene) of North America (Wood and others, 1941). In addition to the two supposed Characidae mentioned above, fishes from Menat have been identified by Piton as *Amia valenciennesi* (Agassiz), family Amiidae; *Chela arambourgi* Piton and *Chela brongniarti* (Agassiz), family Cyprinidae; and *Percilia angusta* (Agassiz), family Serranidae (Piton assigns this to the family Percidae). The identification of an Eocene percomorph from France with a Recent genus (*Percilia*) of fresh-water Serranidae

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[1] Myers (1950) has shown that *Hydrocynus* Cuvier 1817 must replace *Hydrocyon* Cuvier 1819. Usage of *Hydrocionichthys* Travassos for *Hydrocynus* has been discussed by Myers and Weitzman (1960).

known only from Chile (see Eigenmann, 1909, p. 290) should be looked upon with suspicion. Moreover, reference of the supposed cyprinids to the tropical, south-Asian, Recent genus *Chela* should be reinvestigated, especially in the light of the work on this genus and its relatives by Silas (1958).

Professor George S. Myers of Stanford became interested in the presumed fossil characids several years ago, and obtained additional information about them through Miss Marie-Hélène Sachet, of Washington, D. C. Miss Sachet's father, the late Dr. Sachet, was in charge of the collections of the Société Scientifique du Bourbonnais et du Centre de France, Moulins, in which Piton's types were deposited. Through his kindness, and that of Miss Sachet, photographs of the type of *Prohydrocyon pellegrini* were obtained by Prof. Myers. Doctor Sachet informed him that the type and only known example of *Procharacinus arverniensis* was carried away by an officer of the German occupation forces during World War II. Professor Myers has asked me to express his indebtedness to the late Dr. Sachet and to Miss Sachet for their great kindness and aid.

In connection with my osteological work on the Characidae, Prof. Myers has recently turned over to me the information on the type specimens given above and the photographs of *Prohydrocyon pellegrini*. I am greatly indebted to him for this and for his helpful suggestions concerning the present paper.

DISCUSSION OF THE SUPPOSED CHARACINS OF MENAT

In examining the photographs of *Prohydrocyon pellegrini* (Figs. 1 and 2), as well as Piton's original paper (1938), I found good reason to doubt that these fishes are truly characids. A search for characid osteological characters in the descriptions and in the photographs failed to reveal any data to confirm Piton's contention that these are fossil characids.

Piton's descriptions do not include any structural comparisons with characids. With reference to *Prohydrocyon pellegrini*, he said: "Les caractères de ce poisson sort nets. Dents présentes, nageoire adipeuse, mâchoire formeé par intermaxillaires [=premaxillaries] et maxillaires. C'est un *Characinidae* [=Characidae]. Il se rapproche des *Hydrocyoninae* mais il est à peu près impossible de la faire rentrer dans un genre connu." Of *Procharacinus arverniensis*, "Comme la précédente, cette espèce appartient d'une manière indiscutable à la famille des *Characinidae*,....Elle se rapproche également de la tribu des *Hydrocyoninae* sans qu'il soit non plus possible de la classer dans un genre connu." In his descriptions, Piton gave the usual body proportions and fin counts, but did not discuss the osteology. In reading Piton's text one receives the impression that he believed these fishes to be characids merely because they resembled the Cyprinidae (carp-like fishes) but had teeth on the jaws. This is especially apparent from statements in his introduction.

In his text and figures (drawings and legends) Piton made no reference to a Weberian apparatus, and I can find no evidence of one in either of the two photographs of the type of *Prohydrocyon pellegrini* (Figs. 1 and 2). Unless one knows characid cranial osteology very well and has excellently preserved fossils, it is risky to identify any fossil fish as a characid without first identifying a Weberian apparatus. The Weberian apparatus is not always easy to see in fossil characids, but it can often be detected by noting the presence of the neural complex, neural pedicle and short neural spine of the fourth vertebra (Weitzman, 1954, p. 252, fig. 10). I have had no difficulty in identifying these structures in Brazilian fossil characids from the lignite near Taubaté.

The premaxillaries of Piton's fishes are not quite like those of any

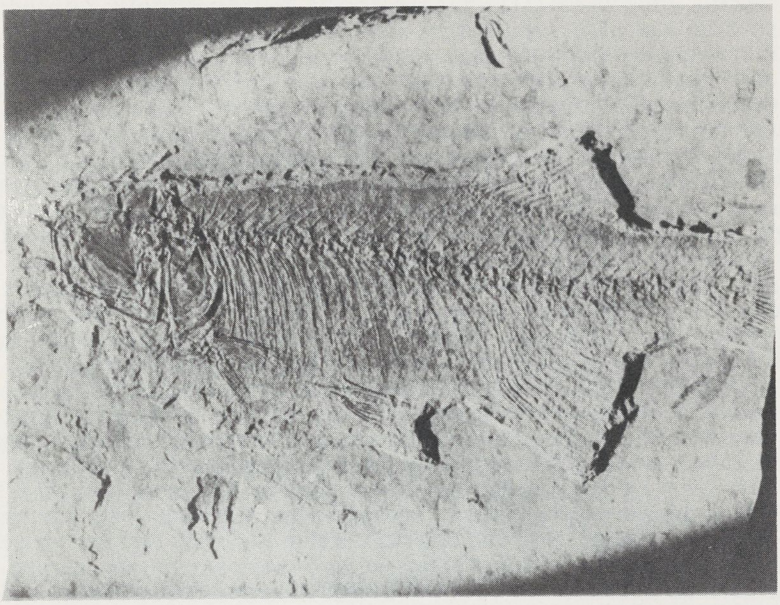

Fig. 1. *Prohydrocyon pellegrini*, Piton, holotype, length 80 mm.

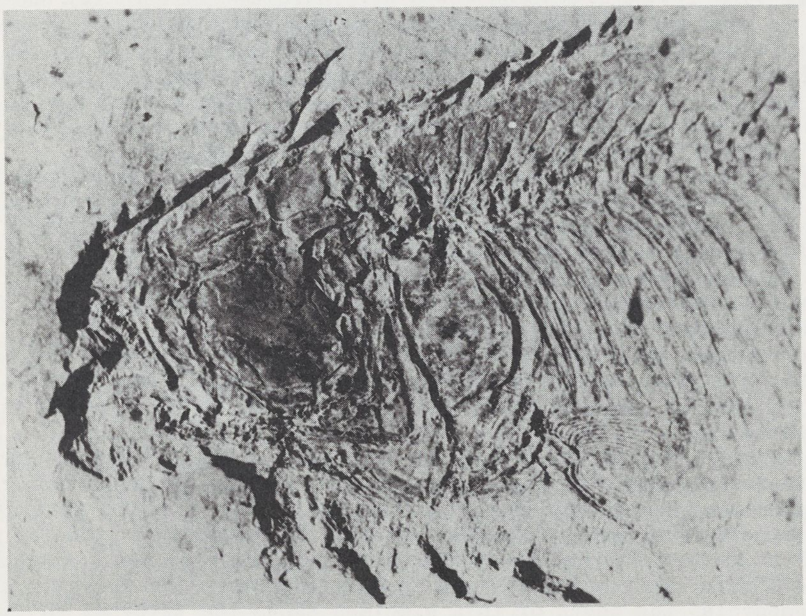

Fig. 2. *Prohydrocyon pellegrini*, Piton, holotype.

Recent characid. His published drawings of *Prohydrocyon* and *Procharacinus* show in both a long premaxillary, almost, if not completely, excluding the maxillary from the gape. A long, tooth-bearing, posterior process of the premaxillary accompanies the maxillary for most of its length. The photographs of *Prohydrocyon* indicate that Piton's drawings are probably relatively accurate with regard to this characteristic. The premaxillary of Recent American characids is almost always short, neither extending posteriorly along the gape, nor almost (if not completely) excluding the maxillary from the gape. In the few American characids in which the premaxillary almost excludes the maxillary from the gape, for example, *Serrasalmus*, *Mylossoma*, *Poecilobrycon*, and *Nannostomus*, it appears to be a specialization in which the premaxillary has increased in size at the expense of the maxillary. There is no long, tooth-bearing process of the premaxillary accompanying the maxillary for most of its length. In African characids, however, Boulenger (1901, pp. 132-135) noted that the maxillary is excluded from the gape in the specialized genera *Citharinus*, *Eugnathichthys*, *Phago*, *Ichthyborus*, and *Neoborus*. In addition, the morphologically conservative African genus *Alestes* has a long posterior process extending along about half to two-thirds the length of the inferior border of the maxillary. In some species of *Alestes* this process may be tooth-bearing. But the maxillary of *Alestes* is not mainly behind or above the premaxillary, as it appears to be in the photograph of *Prohydrocyon*. And in none of the above African characid genera are the premaxillaries and maxillaries shaped like those of *Prohydrocyon*, as illustrated in the accompanying photograph.

Piton gave no information about the teeth except their number and position on the jaws. He did not mention whether they are conical or multicuspid. His drawings show simple conical teeth; presumably this is why he compared his fossils with such characids as *Hydrocynus*, the latter having conical teeth. Myers (1958, p. 29) has suggested that multicuspid teeth on the jaws are probably primitive for characids. If this is true (and the evidence from living characids certainly indicates that it is) one might expect to find multicuspid rather than conical teeth in fossil characids. However, since little is actually known about the evolution of teeth in characids, there being almost no fossil record, it cannot be assumed that there were no characids with simple, conical teeth during the Eocene. Several species and genera of living characids have conical, unicuspid teeth, and such forms may have existed since the Eocene.

In examining Piton's drawings (apparently meant to be reconstructions), I was immediately struck by the very unusual morphological relationships of the bony elements. The drawings are so odd that it seems likely that Piton had little real knowledge of the teleost skull. Moreover, examination of the photographs of *Prohydrocyon* indicates that the errors in Piton's interpretations could not have been derived from moving and damage of bone elements during fossilization.

The drawings show an "occipital" where one would expect to find a parietal, the supraoccipital and the epiotic; a "nasal" where the ethmoid should be located; and an "ethmoid" in the position of the anterior half of the frontal.

In teleosts the metapterygoid is internal to the preopercle and the quadrate usually rests on the dorso-anterior portion of the anterior preopercular arm, never covering it extensively. In Piton's drawing the metapterygoid is shown as lying external to the preopercle, and the quadrate is shown as covering almost the entire preopercular arm. Although in Piton's figure of *Prohydrocyon* the "quadrate" covers the anterior arm of the preopercle, the photo of this specimen shows the external surface of the preopercle to be completely exposed.

The articular of teleosts is a single bone forming the posterior part of the lower jaw. Two large, very elongate articular bones, one placed posterior to the other, are shown in Piton's drawing of *Prohydrocyon pellegrini*. The posterior articular shown in Piton's figure lies inferior to the "quadrate", the latter being in reality the upper part of the anterior arm of the preopercle. As noted above, Piton's posteriorly placed articular appears to be nothing more than the inferior part of the anterior arm of the preopercle. The anterior articular in Piton's figure does lie in the usual position of the articular, but it is probably drawn too long, and the dentary too short. However, examination of the photograph (Fig. 2) gives little aid in determining the relative lengths of the dentary and articular.

SYSTEMATIC POSITION OF *PROHYDROCYON* AND *PROCHARACINUS*

From the above discussion, there seems to be no real evidence that *Procharacinus* and *Prohydrocyon* are characids. Is there any evidence of their true relationships? Fortunately there is. Although these fossils are greatly in need of reexamination, Piton's figures and descriptions, and especially the photographs at hand, suggest that these fishes are members of the Thaumaturidae, an extinct family of presumably salmonoid fishes.

Until recently, the genus *Thaumaturus* had been placed in the Salmonidae. Voigt (1934) described and defined the family Thaumaturidae, and on pages 57 to 62 he gave an account of the systematic relationships of this family. Berg (1940, p. 427) diagnosed the family Thaumaturidae, basing his diagnosis on Voigt's work, and following the latter's lead, assigned this family to the suborder Salmonoidei. However, some aspects of the osteology of the Thaumaturidae as described by Voigt lead me to wonder if the family is correctly placed. For example, the morphology of the maxillary and premaxillary bones, the apparent absence of an orbitosphenoid, and a tendency for the parietals to be separated from each other by the supraoccipital suggest a possible relationship with the haplomous fishes.[2] The relationships of the Thaumaturidae need to be investigated further.

According to Berg (1940, p. 477), members of the Thaumaturidae are known from the Lower Eocene to the Aquitanian [=Lower Miocene] of Western Europe. Piton's fossils were said to be from the Lutetian, which equals the Middle Eocene. This is well within the time-range of the Thaumaturidae. Voigt (1934) described members of the Thaumaturidae from the Middle Eocene Braunkohle of Geisetale, near Halle on the Saale River, in Saxony, Germany.

Voigt's drawings and photographs of *Thaumaturus spannuthi* Voigt show a striking resemblance to the photograph of *Prohydrocyon pellegrini*. Unfortunately, the photographs of *P. pellegrini* do not allow detailed examination of the few cranial characters given by Berg or of the several listed by Voigt. However, Berg stated that the maxillary has few teeth (apparently there are none in Piton's specimens), that it scarcely borders the mouth and that it is mainly situated behind the premaxillary, which does not reach the posterior end of the maxillary; this is true of Piton's figures and of the photograph of the holotype of *Prohydrocyon pellegrini*. Berg called the preopercle "crescent-like", but in Voigt's photographs and drawings (Voigt, 1934, text-fig. 13; pl. 1, fig. 2) it has an acute posterior angle; the preopercle in the photographs of *Prohydrocyon pellegrini* also has an acute posterior angle. Berg listed 40 to 42 vertebrae for members of the Thaumaturidae; Piton counted 40 for *Prohydrocyon*, and examination of the photograph indicates that he was probably correct. The fossil specimen of Piton's other genus, *Procharacinus*, was incomplete, and

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[2] In a paper (Gosline, 1960) received after the present contribution had been written, Gosline, p. 346, also notes that the Thaumaturidae may show more relationships with the haplomous fishes than with the salmonoids. Gosline based his statement primarily on examination of the caudal skeleton.

therefore no vertebral count was taken. The ribs of the Thaumaturidae were characterized by Berg as ossified, strong, nearly reaching the edge of the abdomen; this is true for *Prohydrocyon*, and Piton said that the ribs of *Procharacinus* are strong. Berg (p. 427) said: "Adipose fin described as wanting in Th. spannuthi Voigt and present in Th. intermedius Weitzel." Piton stated that one is present in *Prohydrocyon pellegrini*, but that it is detached from the specimen. The structure he refers to can be seen above the caudal peduncle in Figure 2.

One of the characteristic features of the Thaumaturidae (and its relatives) is the broadness and length of the frontal bones (Voigt, 1934, text-fig. 13; pl. 2, fig. 6); these are present in *Prohydrocyon*, as is well shown in Figures 1 and 2. Also, the general shape of the body in *Thaumaturus* (Voigt, pl. 1, figs. 1 and 2; pl. 14, fig. 2) is about the same as in *Prohydrocyon*. In both, the origin of the pelvics is midway between the origin of the pectoral and anal fins, and the anal origin is below the base of the fourth to the sixth dorsal fin ray.

Thaumaturus spannuthi has 13 to 16 dorsal fin rays, according to Voigt (p. 56); Piton counted 12 dorsal fin rays in *Prohydrocyon pellegrini*. I am unable to confirm Piton's count from the photographs reproduced here, but the number certainly cannot be less than 12. Voigt (p. 57) recorded 14 to 17 anal fin rays in *T. spannuthi*, and Piton recorded a total of 14 anal fin rays in *P. pellegrini*.

The principal caudal fin-ray counts and the caudal fin-ray structure are constant in many groups of living fishes. For example, of over 100 genera and over 200 species of Recent characids that I have examined, all have 19 principal rays - 10 in the upper lobe and 9 in the lower lobe of the caudal fin. Because of the constancy of the caudal fin-ray counts it would seem worthwhile to point out that caudal fin structure and caudal fin-ray counts of fossil fishes should be more carefully determined in the future.[3] Not infrequently these structures are well preserved and they may give excellent clues to the relationships of fossil fishes. Voigt (p. 57) gave 18 to 20 as the principal caudal fin-ray count for *T. spannuthi*; the count for *P. pellegrini*, which I cannot confirm, is a total of 22 principal rays. Piton's formula for the caudal fin count is "4,5-1-20-1-4,5", which I have interpreted as (starting dorsally and continuing ventrad on the fin): from four to five procurrent rays; one long, unbranched ray; 20 branched rays, one long, unbranched ray; four to five procurrent rays. The principal caudal fin-ray count is usually defined as the branched rays plus two (omitting, of course, the procurrent rays). This makes the count of 22 principal rays given above for Piton's specimen.

Lindsey (1955, p. 40) has noted that in *Thaumaturus* the "supraneural" series overlaps the pterygiophores of the dorsal fin, whereas in many other fishes these two series of bones are in a single, continuous series. In all the characid fishes that I have examined, the "supraneural" series and the pterygiophores are continuous, not overlapping. Unfortunately, I am unable to be sure of the presence of a "supraneural" series from the photographs of *Prohydrocyon*. However, when further examples of these fishes become available, the relationships of the "supraneurals" and pterygiophores should be carefully examined.

SUMMARY

In view of the facts discussed above it appears that there is no positive evidence for placing *Prohydrocyon* and *Procharacinus* in the Characidae. The apparent lack of a Weberian apparatus would seem to exclude both of them

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[3] The recent study by Gosline (1960) on the caudal skeleton of isospondylous fishes amply reinforces this view.

from the Characidae. On the other hand, the jaw structure, the large size of the frontal, and the general osteological morphology indicates strongly that these fossil fishes of the Middle Eocene of Europe belong to the Thaumaturidae, a family of supposedly salmonoid fishes (but more probably haplomous fishes) well known from the Middle Eocene of Europe. Lack of direct examination of fossil material precludes a final decision that *Prohydrocyon* and especially *Procharacinus* are synonyms of *Thaumaturus*. However, it is quite possible that *Prohydrocyon*, at least, will prove to be the same as *Thaumaturus*.

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[No date]

Robert E. Vincent

or 3b. If it is logical to assume that those replying to inquiry number one in the affirmative would be against both 3a and 3b, then 899 answers of no to 3a and 899 replies of no to 3b should be eliminated. This would leave a balance of 1,813 for no to 3a, and 1,132 for no to 3b. On this basis the corrected figures would appear as follows:

	Replies			Per cent	
	Yes	No	Total	Yes	No
3a	1,619	1,813	3,432	47.2	52.8
3b	2,016	1,132	3,148	64.1	35.9
	3,635	2,945	6,580	44.7	55.3

The above figures indicate that there is a slight majority against 3a while there is a decided number who favor 3b. The over-all result is that 55.3 per cent of those answering inquiry three are in favor of a change as to issuing separate licenses for deer, elk and bear. The 1,619 replies of yes to 3a and 2,016 replies of yes to 3b also would indicate that there are 397 who favor splitting the license as proposed in 3a, but do not favor the fees as stipulated therein.

SUMMARY

As indicated, it was necessary for us to make certain assumptions, in connection with the questionnaires returned, before we could make an analysis of the results of the survey. Based on our analysis the replies show a relatively strong trend against increasing the license fee to $10.00 (almost (2.5 to 1) and against raising it to $15.00 by approximately 20.6 to 1. All were opposed to both increases about 2 to 1. Those in favor of raising the license fee evidently would purchase licenses at that price, and 146 who were opposed to the increases indicated they would still purchase licenses at the increased prices. A slight majority are against breaking up the resident hunting and fishing license at the stipulated fees (approximately 1.2 to 1). However, there seems to be an over-all preference (approximately 1.2 to 1) for changing the license structure, among those replying to inquiry number three.

The portion of replies returned was 11.67 per cent of the 42,391 resident licenses issued in the state during 1947.

Wyoming Fishes, No. 50

Bluehead Sucker: Western Chiselmouth Sucker: Dwarf Sucker: Mountain Sucker

Pantosteus Delphinus (Cope)

THE BLUEHEAD SUCKER is found in great abundance in the Colorado River drainage, including the Little Snake River, near the mountains. In the headwaters of the Green River it ranks in numbers with the Rocky Mountain whitefish, and it is one of the most important sources of food for the Mackinaw and the larger trouts of other species occurring in the lakes of the upper Green River drainage. Its maximum size is about one foot. When in streams it is usually found in riffle

Inquiry Number One

The replies given to number one in the preceding summary must be revised before any reliable conclusions can be reached. If an individual did not want either increase suggested, he should have answered both a and b in the negative. As there was a total of 1,659 yes answers, out of a possible 4,949, 3,290 were left to say no to both increases, making a total of 6,580 replies of no. A person indicating that he was in favor of the raise to $10.00 would doubtless be against the increase to $15.00. As there were 1,430 favoring the raise to $10.00 these persons obviously were not in favor of an increase to $15.00. Similarly, the 229 replies favoring the increase to $15.00 apparently should have answered no to the $10.00 fee. Thus, the total replies of no should have been 8,239. There were only 6,244. A summary of the above discussion is presented in the accompanying table.

Increase cost of license to	Replies Per Summary Yes	Per Summary No	Error in No	Corrected No	Total Yes & No	Per cent Yes	Per cent No
$10.00	1,430	3,055	464	3,519	4,949	28.9	71.1
$15.00	229	3,189	1,531	4,720	4,949	4.1	95.4
	1,659	6,244	1,995	8,239	9,898		

Out of the total of 4,949 replies 71.1 per cent were against increasing the cost of a license to $10.00 and over 95 per cent indicated that they are in opposition to a $15.00 license fee. Of these 1,430 would favor an increase to $10.00. With a total of 1,659 replies of yes out of a possible 4,949 there are left 3,290 who were opposed to both suggested figures. This means that 66.5 per cent of all those replying obected to paying either the $10.00 or $15.00 license fee.

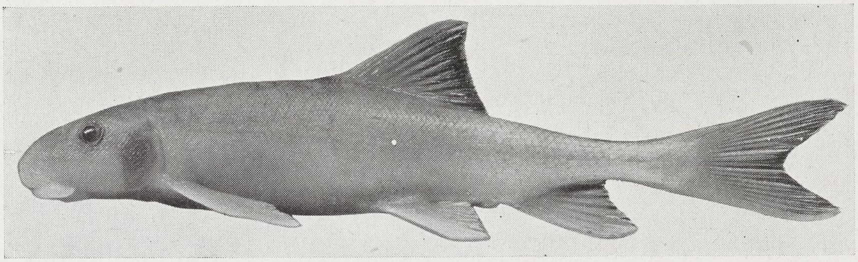
Inquiry Number Two

There were 1,659 answers of yes to question number one, but the summary of replies shows that 1,805 replied with yes and 2,283 with no to inquiry number two. This indicates that some of those opposed to an increase in the license fee would buy one if the raise were made. However, the trend shows quite conclusively that there is considerable opposition to any increase and that many would not purchase a license if the fee were raised. If it is reasonable to assume that those replying yes to question number one would not vote themselves out of the sport of hunting and fishing, then the 2,283 replies of no must have been made by those answering the first inquiry in the negative.

In summary, if the above assumption is correct, the 1,659 in favor of increasing the cost of a license, plus 146 opposing such an increase, would buy licenses at either $10.00 or $15.00.

Inquiry Number Three

Inquiry number three seemingly was misunderstood by a large number of those replying. There were 8,378 answers including both yes and no, and only 6.580 should have been given. Those indicating yes to question number one should not have answered this inquiry. As there were 1,659 replies of yes to number one, only 3,290 of the total of 4,949 should have answered inquiry number three. These should have indicated their reaction to both parts, making a total of 6,580 replies. It is reasonable to assume that the 3,290 who answered no to inquiry number one also replied to question number three. If this is so, 1,798 replies were given by individuals in favor of increasing the cost of a license to either $10.00 or $15.00. With 1,619 replies of yes to 3a, and 2,031 replying no to 3b, 412 of those not in favor of 3b may also object to 3a. With 2,016 answers of yes to 3b and 2,712 answers of no to 3a, 696 not favoring 3a must also disagree with 3b. This makes a total of 1,108 who do not favor either 3a



Bluehead Sucker

areas among the stones.

Ellis (1914) wrote that the stomachs of Colorado specimens contained masses of algae and slime. They have been observed swimming in large schools in the shallows of Lower Green River Lake, where they fed on the algae so abundant on the boulders near the shore. These suckers seem to feed as readily upside down as when upright, and the slime from the underside of a large round boulder can be obtained only by a fish in this seemingly awkward position. The conversion into trout food of algae and slime—food which the trout does not take—is this species' most important contribution to the total value of trout waters. It feeds also to a limited extent on aquatic insect larvae, and is in turn eaten by predatory animals and birds.

Females containing well-developed eggs were taken from Fremont Lake on July 14.

As described by Simon in *Wyoming Fishes,* the body of the bluehead sucker is slender and somewhat compressed in the caudal half. Its head is short, without a fontanelle in the skull. The upper or dorsal profile is sloping, whereas the ventral profile is almost straight. Its snout is broad and heavy, and the eye of moderate size. A large upper lip forms a fleshy hood over the large mouth opening, and the lips are notched at each side of the mouth. Scales are small and crowded anteriorly.

This species is a grayish-blue in general color, darker dorsally. Scales are outlined with dusky. In the spring the sides of the body below the lateral line, especially in the anal region, are pink to orange-red. Pectoral and ventral fins are yellowish. The band of red along the lateral line is interrupted.

The term *Delphinus* derives from "dolphin."

Hunt with Him-Not for Him

"GO HUNTING WITH your boy this year. Then you won't have to go hunting FOR him!"

This advice of Henry P. Davis, public relations division of Remington Arms Company, is worth the serious consideration of every father, guardian or friend of a teen-age American boy.

"All healthy boys have a certain amount of surplus energy which, apparently, they must work off," says Davis, "and sometimes this youthful exuberance carries them into dim and dangerous places strewn with vicious habits. But no one ever heard of a boy who loves to hunt or fish becoming a juvenile delinquent. Real sportsmanship, fair play and a sense of responsibility, all part and parcel of the two sports, cannot walk hand-in-hand with juvenile delinquency. They speak a different language.

"Hunting is the oldest of all sports. Long before the practice became a sport, man was forced to hunt for his very existence. For centuries the sport has had a strong appeal to men, women, youngsters . . . rich and poor alike. Every section of this country, even though comparatively new, is steeped in the traditions of the chase. And despite the fact that game supplies are no longer as plentiful as in former years, the thrill of the hunt grows stronger, for the sportsman must exercise a greater amount of skill than ever before if he is to reap a sporting share of the annual wildlife harvest.

"One has only to expose the average American youth to the multitudinous charms of the outdoors and the many attractions of the hunt to imbue him with the desire to become a sportsman," continued Davis. "Teach him that the greatest fun is to be found in the finding of the game, not in the taking, although the latter, in fair measure, is the final desire. Point out the many little things which contribute to the pleasures of the hunt. Show him how the hand of Nature weaves her many wonders . . . small things entirely overlooked by the casual observer. Answer his countless questions . . . as best you can, for you can rest assured his quick young eyes and grasping mind will bring simple queries which, indeed, will tax your own knowledge of woods lore and natural history.

"Encourage him to ask these questions, for from them you'll learn many things yourself. And by his very inquisitiveness he will indicate his intense interest.

"When you take a boy hunting you pay him the greatest compliment. You are treating him like an equal, and no boy can fail to appreciate this tribute. He knows that the possession of a gun carries with it a grave responsibility, and he is anxious to learn to use it safely and properly. He is proud of the fact that you expect him to act like a *man* and he revels in your confidence.

"Hunting will not only give him a sense of responsibility but will teach him fair play in his relations with mankind and wildlife alike, create a respect for the property rights of others, bring to him a realization of the necessity of conserving our natural resources and set his feet in the path of clean living and clear thinking.

"Don't make his first day's hunt too long. Try to take him into good game country on the first trip and do not allow him to become too tired. Make every trip a real adventure . . . and end it just when he wants a little more.

"If you have fair luck, all well and good," concluded Davis. "But cause him to realize that good sport is to be truly appreciated and that, whether the game bag be full or empty, there's a lot of fun in *just hunting*. He'll glory in recounting his experiences to his pals. He'll grow closer to you and you'll become even a bigger hero to him than you now are. No, you won't have to go hunting *for* him if you'll only take your boy hunting *with* you this year."

The wolf spider, only about an inch long, often carries its young on its back until they can fend for themselves. A brood will sometimes number as many as one hundred and twenty-five.

Raccoon gets its names from the fact that it washes its food before eating it. The name raccoon is a derivation of the Indian name "arathcone" meaning "the washer."

The southern fox squirrel is the only squirrel in America which has a white nose and white ears.

[no date]

RESEARCH ON ENDANGERED FISHES IN THE NATIONAL PARKS WITH SPECIAL EMPHASIS ON THE DEVILS HOLE PUPFISH

James E. Deacon and Maxine S. Deacon[1]

Fishes living in National Parks of the Western United States have physically adapted to the torrential currents, and shifting, unstable substrates of the Colorado River. They have developed humps, apparently for stability at the bottom; fusiform bodies, with slender caudal peduncles and expansive fins for maximum power in the swiftly moving current; large size, including the largest minnow in the world at more than eighty pounds; reduced or embedded scales, and relatively small eyes, characteristics of fishes living in silt-laden streams. Most of these features are expressed to varying degrees by the native fishes inhabiting Grand Canyon National Park.

The most extreme hump is exhibited by the humpback chub, *Gila cypha;* the most extreme fusiform shape by the bonytail chub, *Gila elegans;* and the largest size by the Colorado Squawfish, *Ptychocheilus lucius*. Both above and below Grand Canyon National Park the bizarre razorback sucker, *Xyrauchen texanus*, occurs, apparently having adapted to less torrential stretches of the river. This species occupies some reservoirs of the mainstream Colorado. Its decline and extinction in many reservoirs built within its native range, but its persistence in others, remains a puzzle. Some information is available on spawning, feeding, and relative abundance in some areas. It has also been successfully spawned and reared in hatcheries.

At a quite different physical extreme, we also have fishes adapted to the extreme ranges of variability in salinity, temperature, and quantity occurring in the waters of Death Valley National Monument. Here are species of the genus *Cyprinodon* living in waters that occasionally form a thin film of ice in the winter, and reach maximum temperatures of about 43°C (109°F) in summer. The salinities range from relatively low to concentrations several times that of sea water. Salt-encrusting algae form steep-sided, shallow pools which eventually build a roof of salt. Occasional flash floods may sometimes turn an isolated pool, a few meters in length and a few centimeters in depth, into a portion of a river over a hundred miles in length. Seasonal variations in evapotranspiration isolate some portions of a creek as small, warm, increasingly saline pools. In such habitats, the importance of surviving a few hours during the hottest part of the day becomes critical. The zone of resistance (Fry, 1971) or resistance time (Brett, 1956) therefore, may be one of the most important adaptive features of this group. On a longer time scale, in the Death Valley region, climatic shifts have created at Devils Hole what may be the smallest habitat in the world containing the entire genome of a vertebrate species.

Man's competition for water has pervaded every aspect of his occupation of the western United States. Irrigation practices required establishment of a set of societal rules almost as soon as irrigation began. A major portion of our present federal and state water law was developed in response to the demands to formalize the right of landowners to the surface and subsurface waters on their lands. As the resource became reduced, competition for the resource increased and society was forced to establish priorities and make hard decisions relative to its use.

During the expansionist period of settling the west, society's definition of "good" heavily emphasized the values of economic and population growth. More recently we have been shifting our definition of "good" toward more qualitative values. Not surprisingly this shift toward quality involves the necessity to mediate through the courts, the inevitable conflicts that arise between adherents of the expansionist philosophy and those who believe that quality of life is society's most pressing need. The reflection of these societal values in judgments being handed down by the courts is evident in the clear and concise but eloquent language of Federal District Judge Roger Foley of the District of Nevada. In his Findings of Fact and Conclusions of Law which appeared in a permanent injunction granted by him on 9 April, 1974, Judge Foley wrote as follows: "The United States has shown that the public interest lies in the preservation of this endangered species. Congress has enacted the Endangered Species Conservation Act (16 U.S.C. 688aa.), and the Secretary of the Interior pursuant to that statute has identified the Devils Hole pupfish, *Cyprinodon diabolis*, to be an endangered species. Witnesses offered by the United States testified to the importance of the species to mankind. Congress, state legislatures, local governments, and citizens have all recently voiced their expression for the preservation of our environment, and the destruction of the Devils Hole pupfish would go clearly against that theme of environmental responsibility."

Defining, interpreting and demonstrating the benefits to be gained through practicing environmental responsibility may be the most important contribution the National Park Service can make to the future of the U.S.A. The Park Service has played a key role in reorienting the administration of the waters of the West toward increased recognition of qualitative values in the environment. The Devils Hole pupfish case stands as a landmark! The Park Service will continue to play an important role in establishing priorities for the use of water in the West. It is currently widely assumed that if water is needed for people, the people will get it -- somehow! What is less well understood is that the people *need* the water for purposes other than drinking, irrigation and power. These other qualitative needs are beginning to be established, and the National Park Service is and must continue to play a central role in that trend.

It has been well established that the large main-stream dams on the Colorado have caused significant detriment to the native fishes (Vanicek, 1967; Vanicek and Kramer, 1969; Vanicek *et al.*, 1970; Holden and Stalnaker, 1975). In addition to interrupting movements of native fishes which may have been necessary for successful spawning, dams have significantly lowered the water temperatures downstream, in many cases

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precluding successful spawning of native fishes. In Grand Canyon, the closure and operation of Glen Canyon Dam has resulted in a significant lowering of water temperatures downstream. Some introduced fishes, such as carp, red shiner, and green sunfish have been pushed downstream by the lower water temperatures. At present, it appears that the introduced forms in Grand Canyon may have been more adversely affected than the native forms (Figure 1). Collections of fishes made in 1968 show most introduced forms occurring upstream to Lee's Ferry, just below Glen Canyon Dam. Summer water temperatures below Glen Canyon Dam dropped from about 20°C in 1968 to about 10°C following achievement of full pool level in Lake Powell, and fish collections subsequent to 1968 show some introduced forms occurring further downstream or restricted to mouths of tributary streams. By contrast, the native fishes have not shown such severe downstream restriction although they have declined somewhat in abundance. This relationship should be watched closely in the future since it could be quite significant to the survival of the threatened and endangered fishes living in Grand Canyon. For example, the native fishes may simply have longer life spans than the introduced forms and, therefore, require a longer period of time to show the detrimental effects of lowering water temperatures. It is also possible, however, that the native species have found suitable spawning areas in tributary streams or elsewhere in the mainstream and that adults are better able to survive in the cold tailwaters than are some of the exotic species. Recent collections leave little doubt that the lower little Colorado River is important to the humpback chub, *Gila cypha* (Suttkus and Clemmer, personal communication; and R.R. Miller, personal communication).

It may be especially significant that Grand Canyon is not being intensively managed to enhance the sport fishery for cold water game fish. Thus, the native fishes are apparently competing primarily with warm water species that have moved upstream from Lake Mead. It is commendable that the National Park Service has sponsored studies that have developed a reasonably good data base on the fishes of Grand Canyon National Park and obvious that additional information on life history of the native species is needed to develop management alternatives that would insure their continued survival.

It seems especially important to examine the thermal ecology of the native forms. Where and at what temperatures they spawn, pass the fry and fingerling stages, and what their thermal tolerance limits at all stages of the life history are. The intriguing point is that there seems to be a possibility that we may be able to manage the waters within Grand Canyon to enhance the native species.

Probably the two most striking features of the environments in which pupfishes of Death Valley have evolved are the highly variable conditions of temperature and salinity. Much attention has been directed to the constancy of the head spring environments. The fact that much tectonic activity is, and for at least the past few million years has been, occurring in the Death Valley region suggests that most head springs are probably quite transitory. The differentiation that has taken place among the pupfishes, therefore, has probably been most influenced by the variable conditions of temperature and salinity characteristic of the marshes.

The critical thermal maxima for *C. diabolis*, *C. milleri*, and various populations of *C. nevadensis* have been determined by Brown and Feldmeth (1971), Otto and Gerking (1973), and James (1968) to be about 42-44°C. Maxima for long term survival probably are near 38°C. Low temperature tolerance is less well documented but in most cases is near 2°C. Brown and Feldmeth *(op. cit.)* viewed C. diabolis as having evolved in a thermally constant environment, similar to the present condition of Devils Hole. This interpretation may be untenable in view of the clear evidence of higher water levels in Devils Hole, and the evidence developed by Mehringer and Warren (1976) of marked changes in water availability in the Ash Meadows area over the past several thousand years. While the species is strongly differentiated and has probably been isolated from other pupfish populations in Death Valley longer than other forms, its habitat may also have been thermally variable.

Observations of responses of *C. n. nevadensis* to thermal variations at Saratoga Springs, Death Valley National Monument (Deacon, 1967, 1968) follow closely results of experimental determination of CTM. Fish have been seen swimming voluntarily at temperatures between 8° and 42°C. They occasionally dart quickly in and out of areas in the marsh with temperatures up to 44°C. At temperatures below 7°C fish are not seen in the marsh but can be collected by seining through the soft bottom mud. Measurements of diel activity as expressed by catch per trap hour in the marsh at Saratoga Springs illustrate the influence of temperature on activity. On 25-26 January, 1967, temperature at the mud-water interface in the marsh fluctuated between 15° and 23°C. These temperatures are within the mid-range of thermal tolerance for *C. nevadensis*. Catch rate shows a distinct bimodal pattern with peak periods of activity in morning and evening (Figure 2). This is also the basic pattern expressed under normal conditions, in the main spring pool (Figure 3) where water temperatures fluctuate narrowly between 26.5° and 31.0°C throughout the year. During summer, water temperatures in the marsh commonly exceed 38°C during mid-day and mid-day depression of activity remains evident, perhaps in this instance enforced by high temperature (Figure 4). While no activity occurs at the minimum winter temperatures, a single daily activity peak occurs in the early spring as the water begins to warm up. This condition is evident from data taken on 24 March, 1967 (Figure 5). Thus, it appears that *C. n. nevadensis* exhibits a bimodal pattern of diel activity under moderate temperature conditions and that at temperatures below 15° and above 38°C, activity is reduced or ceases entirely.

Similar observations have been made on *Crenichthys baileyi* and *Crenichthys nevadae* (Hubbs and Hettler, 1964; Hubbs *et al.*, 1967; and Deacon and Wilson, 1967). In those species activity is restricted at high temperatures and low oxygen concentrations. It seems probable that scope for activity will be reduced as either thermal or oxygen stress is placed on the individual. For example, since reproductive behavior is metabolically demanding it will be abandoned as scope for activity is reduced. Similarly, since feeding probably occurs primarily during peak activity, metabolic demands for assimilation will likely reach a peak a short time after peak activity has occurred. If, as Fry (1971) suggests, the metabolic cost of assimilation reduces the scope for activity, it is reasonable to expect minimum activity during a period of food assimilation, especially when the CTM is closely approached. The same result (reduced activity following feeding) could also be expected under conditions of high salinity if osmoregulatory demands effectively reduce scope for activity. These are both potentially fruitful research opportunities for fishes living in osmotic or thermally stressful environments, such as occur in Death Valley National Monument.

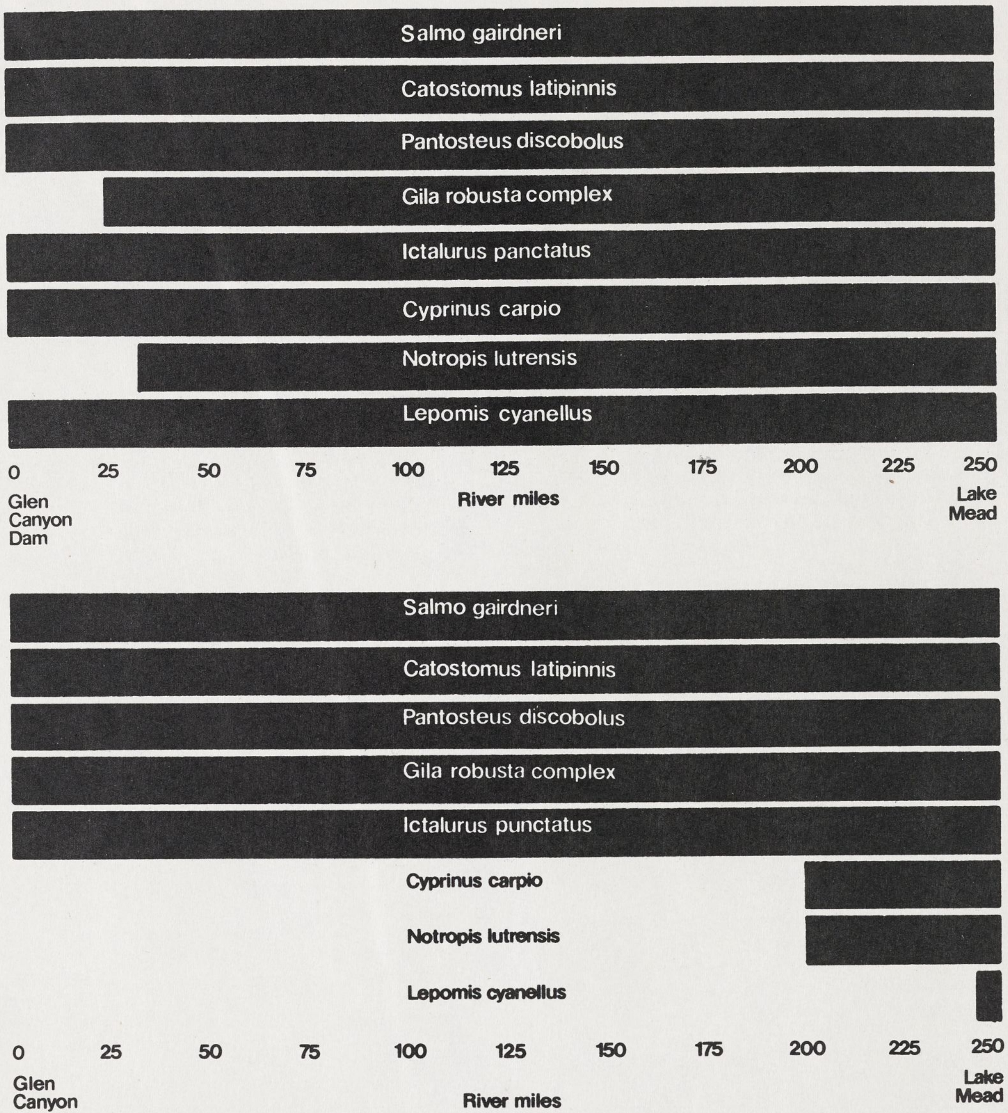

FIGURE 1. Distribution of some native and introduced fishes in the mainstream Colorado River in Grand Canyon, 1968 (upper) and 1975 (lower).

Defense of territories and presence of breeding colors during the summer is common in the marsh at Saratoga Springs until mid-day temperatures rise above 35°C. No fish were seen defending territories or with well-developed breeding colors at temperatures above 38°C (Figure 4). Shrode (1974) showed that eggs of *C. n. nevadensis* would develop at constant temperatures between 20° and 36°C (but not at 38° and 18°C); however, development would occur when temperatures fluctuated between 30-38°C, 20-28°C and 28-36°C. Clark Hubbs (personal communication) has recently shown that *Cyprinodon* eggs will develop up to a constant temperature of 37°C. Thus, it appears that reproductive activity is discontinued at temperatures which rise above those compatible with normal egg development. Furthermore, the primary spawning period occurs during spring and early summer when environmental temperatures never exceed limits compatible with development. Occasionally during mid-summer, environmental temperatures may exceed 38°C and result in egg mortality in the marsh habitat. Shrode's data indicate that developmental temperature tolerance of *C. n. nevadensis* is unusually wide, a situation that is also true for adult pupfish. On the other hand, Gerking (personal communication) has recently shown that critical thermal limits for ovulation of normal ova in this subspecies are quite narrow. Critical thermal maxima for young pupfish exceed that for adults. Thus, under maximum thermal stress, egg mortality will be followed by adult mortality, while young fish will survive the longest. Critical thermal maxima for two-month-old fish acclimated to 36°C was determined by Shrode *(op. cit.)* to fall at about 44°C.

Man induced changes in the Death Valley region have been rapid and with far-reaching consequences. Because all individuals of distinctive species or subspecies occupy very restricted habitats in this area, the changes have more rapidly affected the entire population than has been the case in larger, and more diverse habitats of the Colorado River system. Illustrative of these changes is the extinction in 1958 of both *Empetrichthys latos pahrump*, formerly occurring only at the Pahrump Ranch, Pahrump Valley, Nevada. Irrigation withdrawals resulted in drying up the only springs containing populations of these subspecies (Minckley and Deacon 1968). Except for two transplanted populations, one at Corn Creek Spring, Clark County, Nevada, the other in a plunge pool on the Lake Mead National Recreation Area, the third subspecies, *E. l. latos*, and last remaining representative of the genus living at Manse

(Bowman) Ranch, Pahrump Valley, Nevada, would have suffered the same fate during the summer of 1975 when the last remaining natural habitat occupied by the genus *Empetrichthys* temporarily dried up as a result of irrigation withdrawals.

Except for successful litigation which went through the U.S. Supreme Court, a similar fate would, in all probability, have been the lot of the Devils Hole pupfish. This species is restricted to a single limestone cavern in Ash Meadows, Nevada. The cavern system was made a disjunct portion of Death Valley National Monument in 1952 by President Truman. Information on population sizes is available since 1967. Beginning in April 1972, scuba divers have been used to assist in visually counting the population throughout the entire depth of Devils Hole in which it occurs. The cavern system is quite extensive, and is only incompletely mapped (Figure 6); however, *Cyprinodon diabolis* occurs only in the area of sunlight penetration. While it regularly occurs down to 26 m the population is far more concentrated near the surface. Water temperature in nearly constant at 33°C, and other physical and chemical characteristics of the water are also nearly constant (Dudly and Larson 1974). Since the water surface is about 23 m below the contour of the mountain in which the hole occurs, the water surface receives little sunlight. The time during which sunlight falls on the water surface changes seasonally, resulting in marked seasonal variation in primary productivity.

Beginning in 1969, significant variations in water level were superimposed on the seasonal variations in sunlight as a factor of primary importance in controlling population size of *C. diabolis*. These changes have resulted from ground water pumping in the nearby aquifer (Dudley and Larson, 1974). The purpose of pumping is for irrigation of pasture and hay crops to be used for raising cattle.

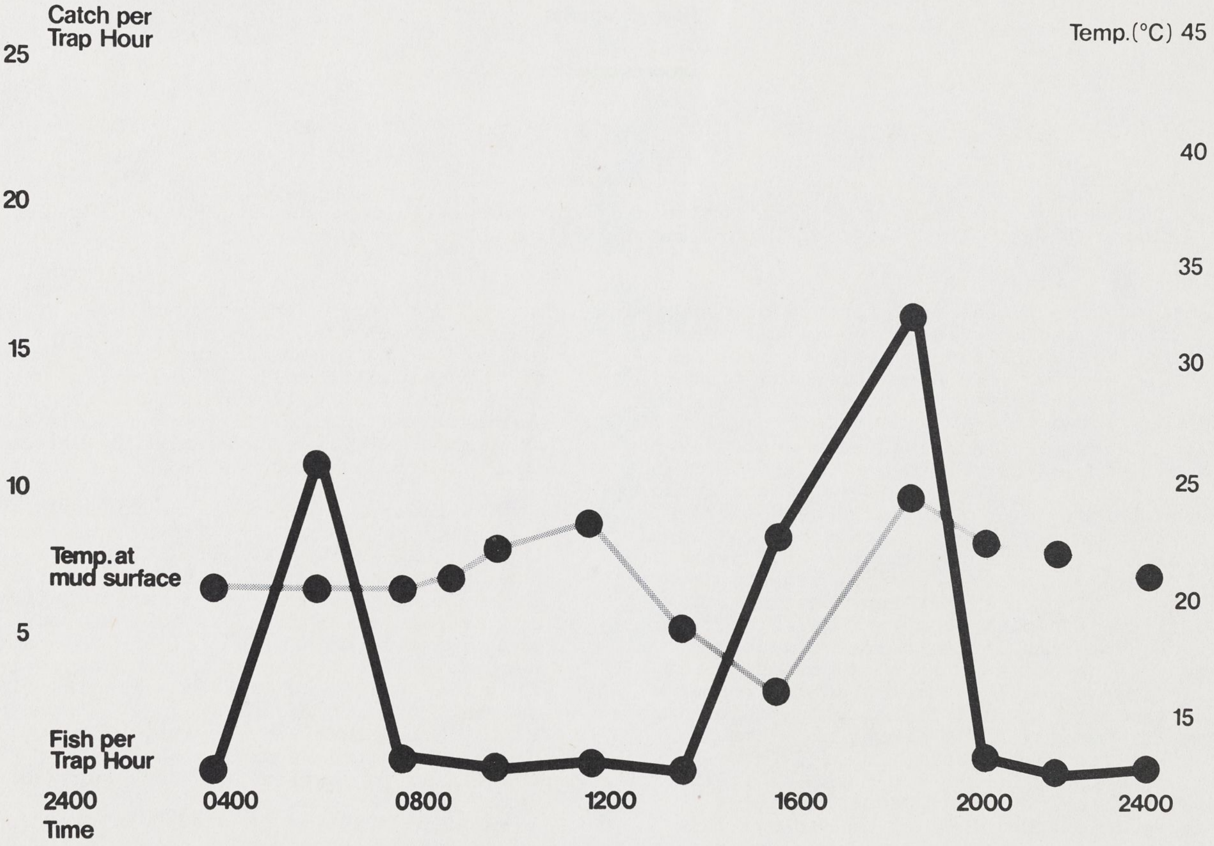

Figure 2. Diel variation in catch per trap hour in the marsh at Saratoga Springs, D.V.N.M. 25-26 Jan. 1967
Water temperature -15 -23 °C.

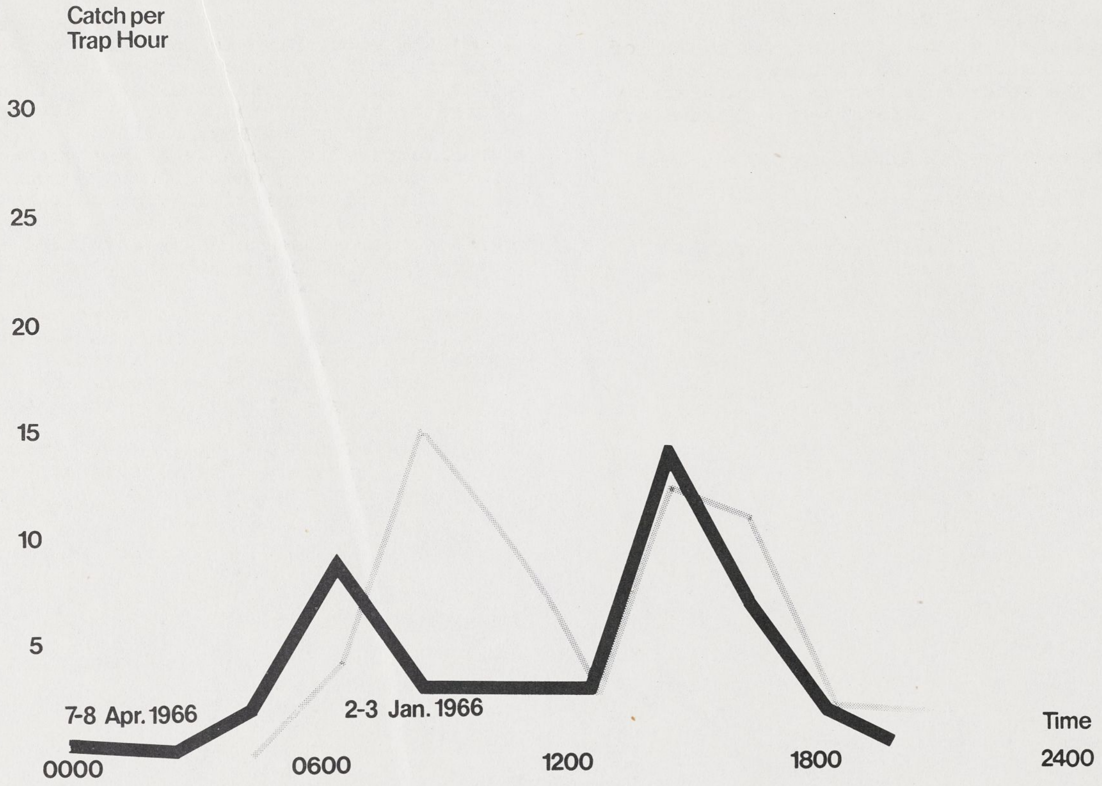

Figure 3. Diel variation in catch per trap hour in the constant temperature main spring pool at Saratoga Springs, Death Valley National Monument. Water Temp. 26.5–29°C.

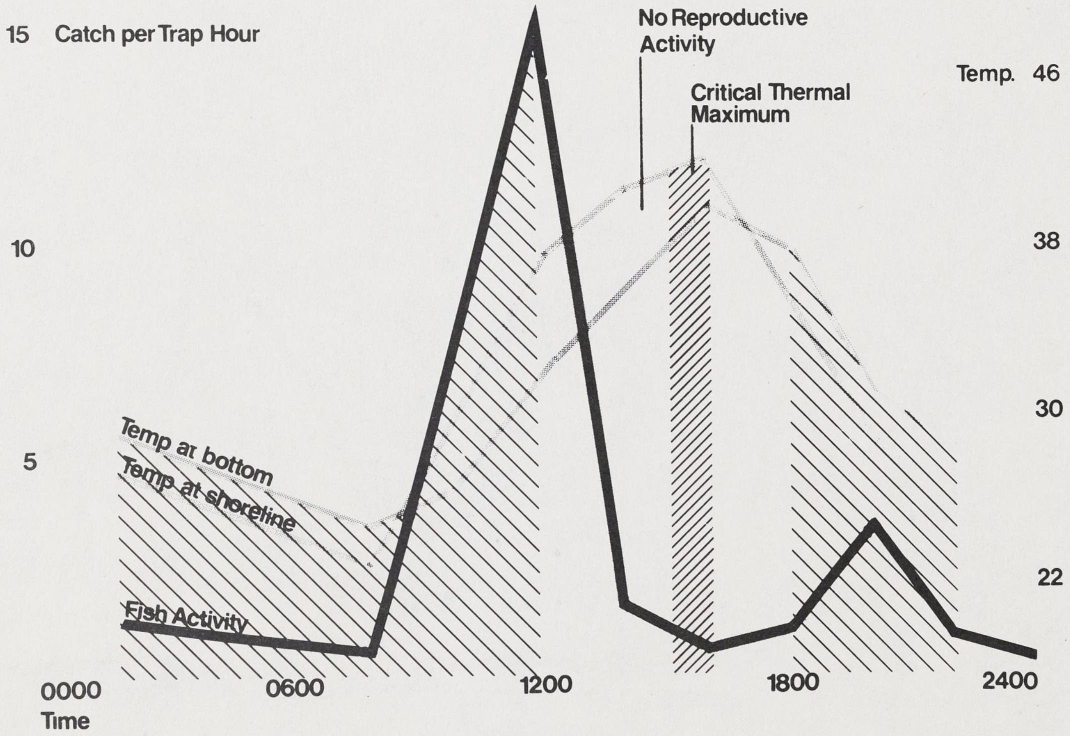

Figure 4 Diel variation in catch per trap hour, reproductive activity and temp. in the marsh at Saratoga Springs, Death Valley National Monument, 18 August, 1966.

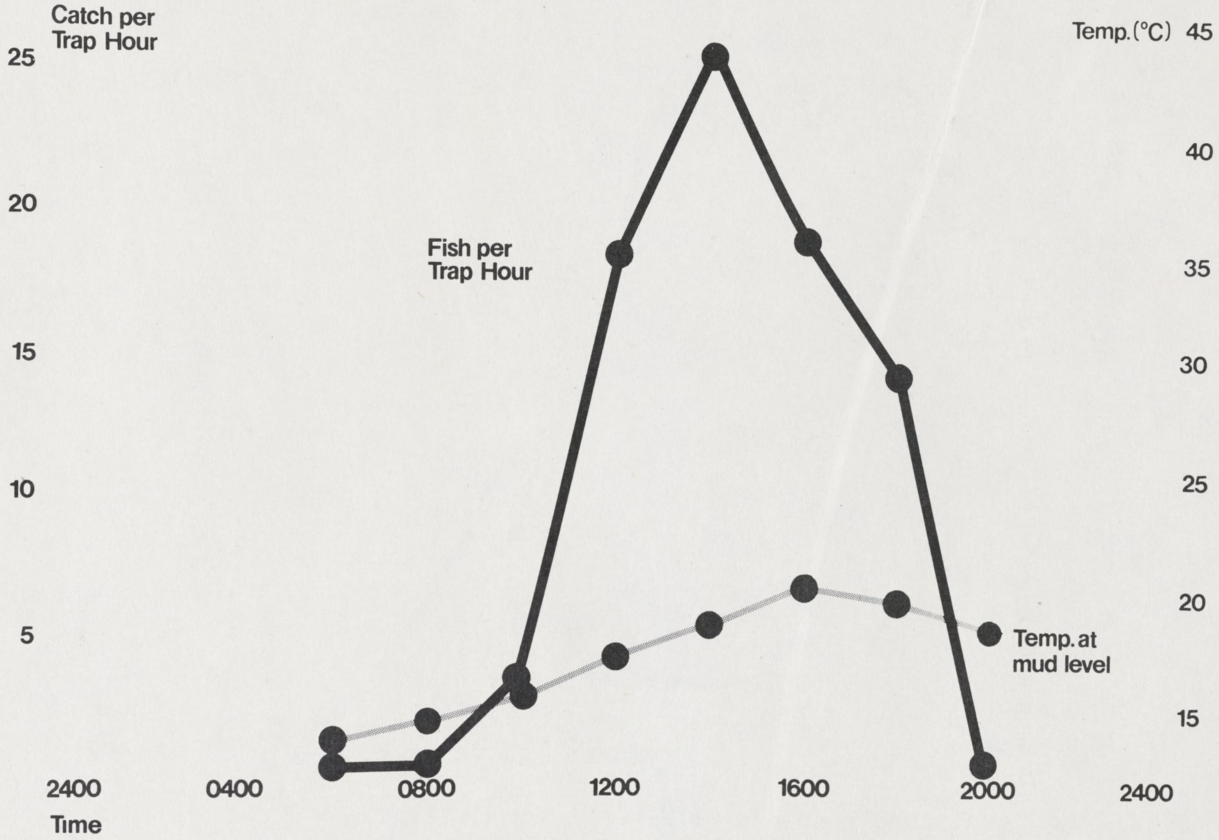

Figure 5 Diel variation in catch per trap hour in the marsh at Saratoga Springs D.V.N.M. 24 March 1967

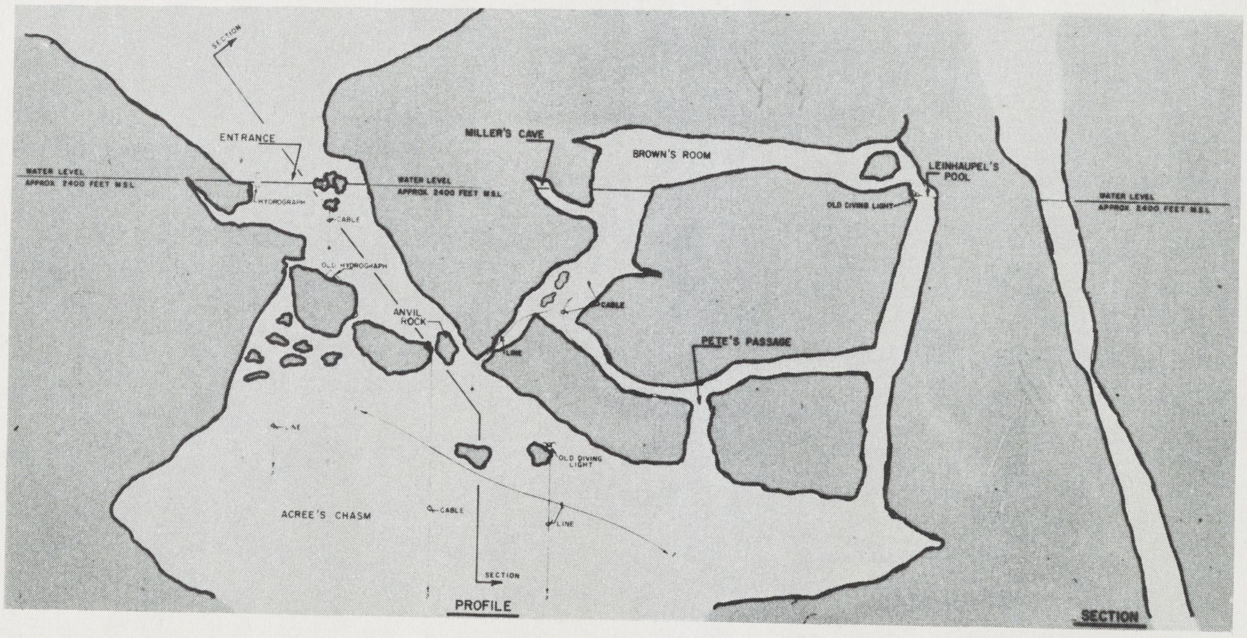

Figure 6 Vertical section of Devils Hole, Death Valley National Monument.

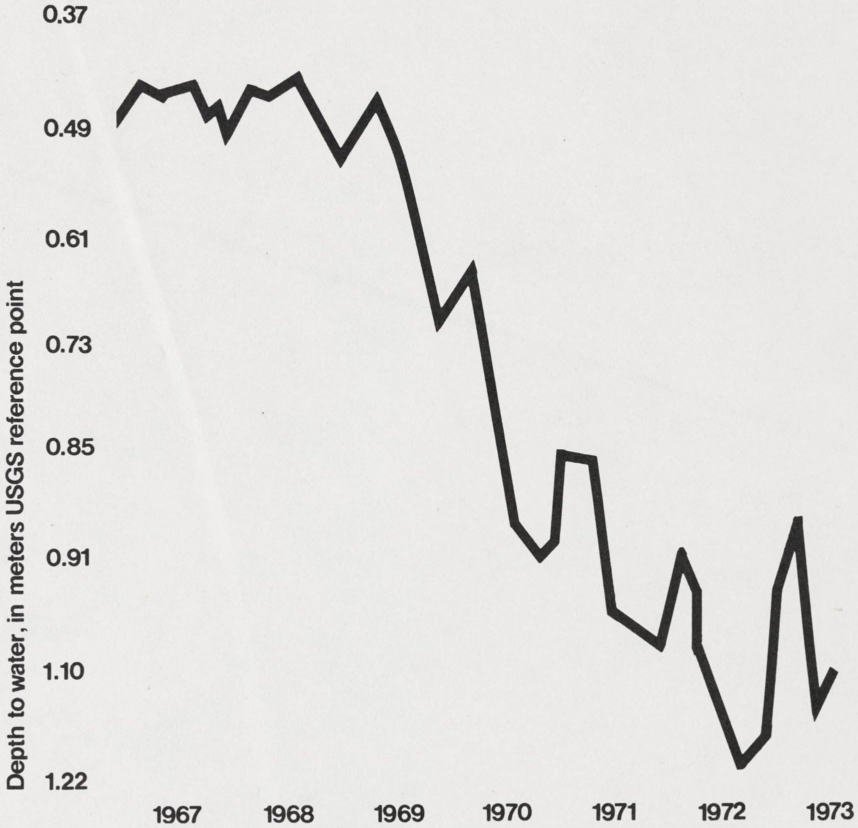

Figure 7. Monthly low water levels at Devils Hole, 1967–73.

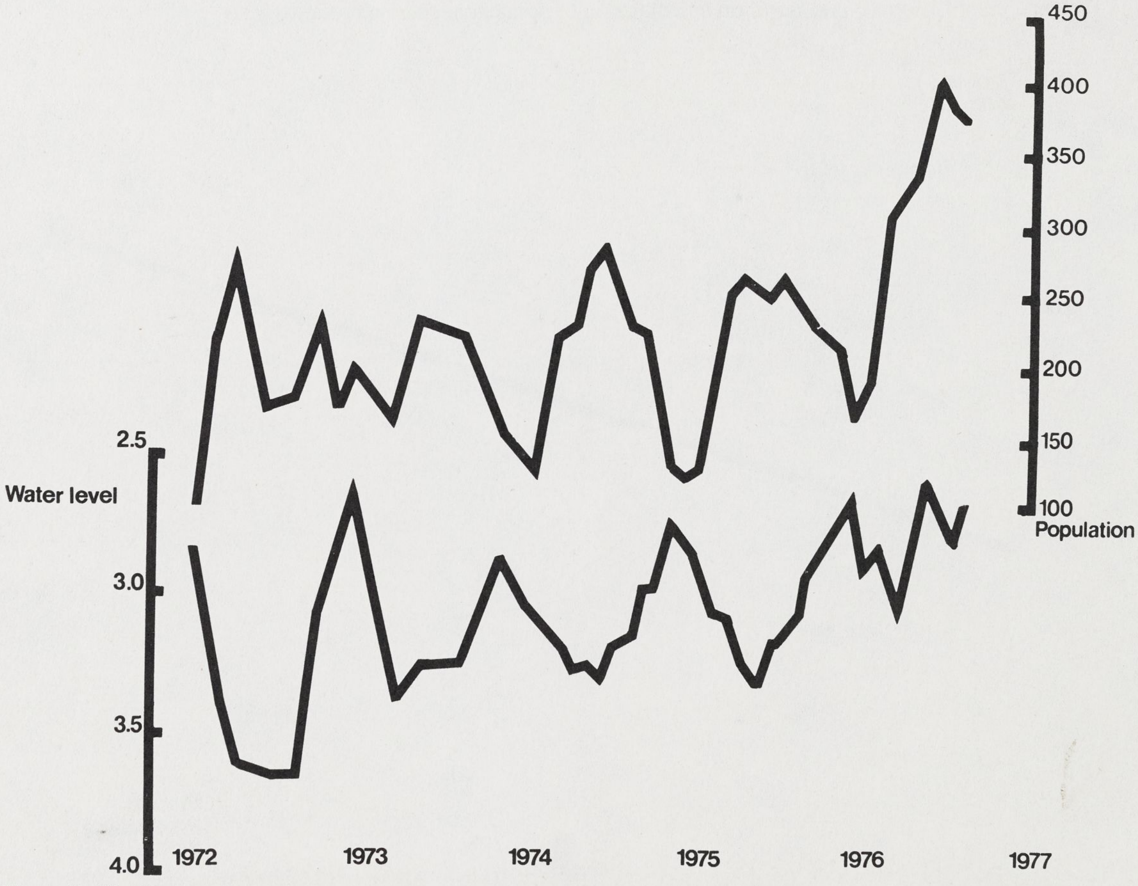

Figure 8. Fluctuations in estimated population sizes of juvenile and adult Devils Hole pupfish, April 1972 — Dec. 1976.

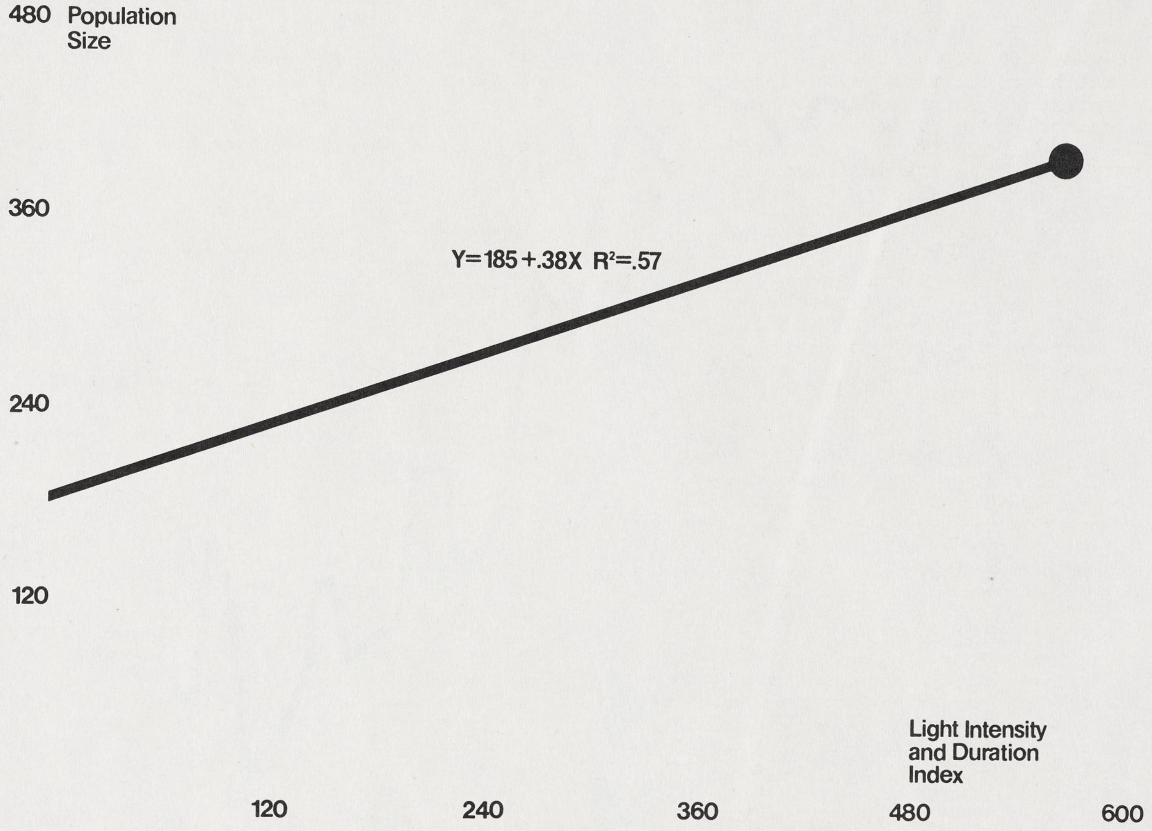

Figure 9 Light intensity and duration correlated with population size two months later.

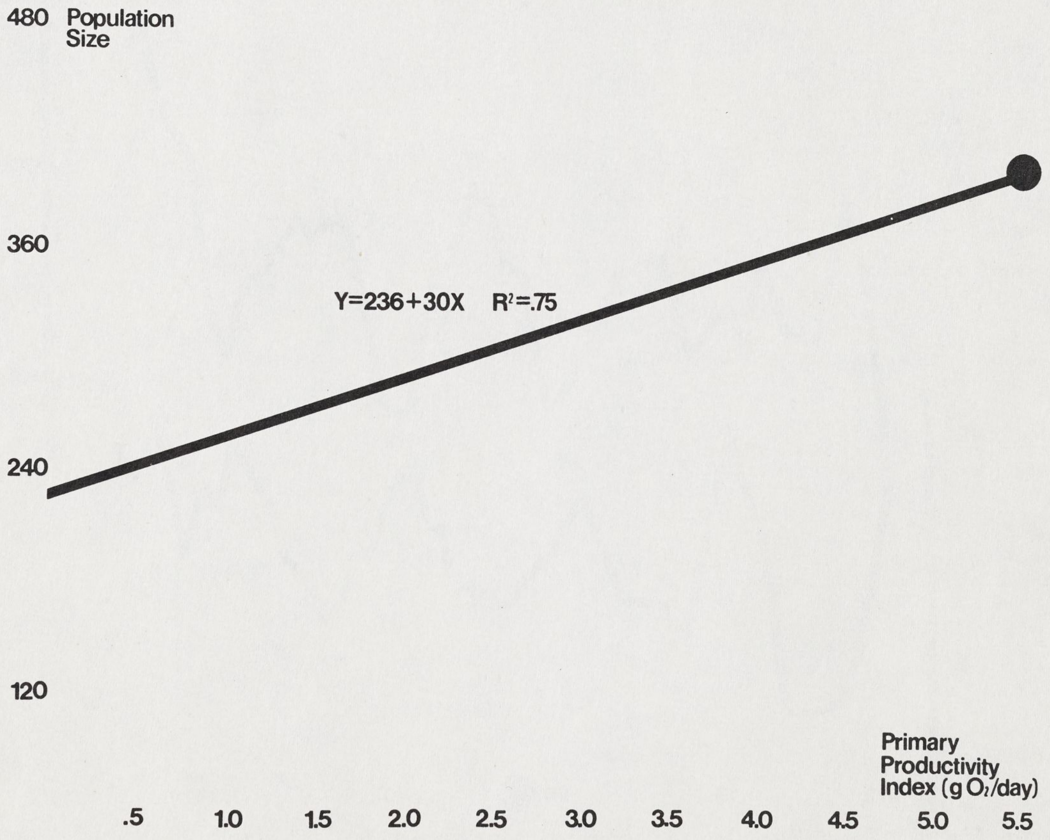

Figure 10 Primary productivity index correlated with population size one month later.

On 20 September, 1972, water level in Devils Hole reached its historic minimum of 1.19 meters below a USGS reference point installed on the rock wall above the water surface. This was the culmination of a downward trend that became evident in 1969 (Figure 7). Frequent census data beginning in April 1972 (Figure 8) shows that, beginning from what was probably an all-time historial low population (of juveniles and adults), the population increased to July 1972. Between July and September, as the water level fell to its lowest point, the fish population also crashed. During this period, subsequent and prior data indicate that a continued population increase would normally be expected. The crash, therefore, is probably attributable to a reduced carrying capacity resulting from low water levels. At the low point, all of the loose gravel and rubble that could reasonably be removed, was removed from the natural shelf in an effort to increase the available habitat. In addition, artifical lights were installed in hopes of increasing the primary production. The fish population responded by increasing its numbers to about 250 by January, 1973. At that point the artificial lights were turned off, and the water level continued to rise. Within a month the population had declined. By March, probably because of the onset of spawning (Minckley and Deacon, 1973), a slight increase was noted. Between March and June when the next census was taken, a flash flood carried large amounts of debris down onto the natural shelf, and NPS personnel, in order to enlarge the habitat, again removed the debris. The result was that during this period, rather than exhibiting its normal spring increase, the population declined. On June 5, 1973, the court appointed a Special Water Master to oversee a permanent injunction granted on that date. The injunction was for the purpose of maintaining sufficient water in Devils Hole to tend to insure the survival of *C. diabolis*. From that time until July 1976, the water level was managed so as not to fall below 1.01 meters below the USGS reference point. The result has been that since June 1973 there has been a relatively regular fluctuation in population size. On 2 July, 1976, the water level began to be managed so as to remain above .91m. Actually water levels rose to about .82m below the reference point. The population responded by increasing to about 400 individuals on September 24, 1976 (Figure 8).

We believe to tend to insure the survival of the species, the minimum population size should not fall below 200 individuals. It appears that the maximum population is about twice the minimum. Therefore, a desirable maximum should fall at about 400 individuals.

We have some information (less precise for 1967-68 than for 1972-76) on maximum population sizes prior to pumping and, therefore, can arrive at some estimates of the requirements for achieving a summer maximum of 400 individuals on the basis of regression analysis. Using data available on maximum population size and water level for 1967, 68, 72, 73, 74, 75 and 76 we find a correlation coefficient of .86 with an R^2 of .73 at the 95% level of confidence. This suggests that a maximum population of about 400 individuals could be expected at a water level of about 0.73 meters.

Data on population sizes for 1972-1976 are more accurate as mentioned previously. If we eliminate the less accurate 1967 and 1968 data and examine only the better data, we again find a high correlation coefficient of .81 with an R^2 of .65 at the 95% level of confidence. Note that the slope for this line is somewhat steeper than was previously true, indicating a more pronounced effect of water level on population size. Again, however, we find that a maximum population size of about 400 individuals can be expected at a water level of about .73 meters below the reference point.

The influence of seasonal variations in light duration and intensity on population size of *C. diabolis* is evident from data acquired in 1975-76. Pyrheliometer recordings show that, with a lag time of about 2 months, population size increases as sunlight duration and intensity increases. The relationship is strong with a correlation coefficient of .76 and an R^2 value of .57 at the 95% level of confidence (Figure 9).

A third and perhaps even more directly influential parameter affecting population size is the total primary productivity of the area circumscribed by the natural shelf. We have developed a PPR index based on diel fluctuations in O_2 content of the water. This information, however, is limited to the months of May through October since sunlight intensity and duration on the water surface during other times is insufficient to stimulate sufficient primary productivity to be measureable using our present methods. The data do show, however, that, with a lag time of about 1 month, population size increases as the primary productivity index increases (Figure 10). The correlation coefficient of .86 with an R^2 of .75 at the 95% level of confidence again suggests a relatively high correlation for a natural system.

The primary productivity index is based on fluctuations in concentration of dissolved oxygen over the natural shelf. As the volume of water over the natural shelf increases, a larger biomass of plants can be accommodated and, to that extent, the volume of water over the natural shelf may also influence the primary productivity index. In effect, this means that as water volume increases, potential for primary production also increases. This potential is realized only when the sun's rays are able to fall on the water surface. Total production of the pool thus can be maximized only by increasing the water volume during a period of increasing light intensity. Since typically during the period 1970-76 water volumes have been decreasing during periods of increasing light intensity, it is evident that the decreasing water levels have caused a depression in the population size that would have been reached under more stable conditions. The important point demonstrated is that increasing sunlight appears to stimulate increased production which in turn results in increased numbers of fish.

The regression formula of primary production on fish population size suggests that a productivity index of 5.47 grams O_2 per day is necessary to achieve a maximum summer population of about 400 individuals. Frequent measurements of the primary productivity index from 26 July - 3 September 1976 show that total production estimates over the shelf ranged between 1.8 and 5.5 gO_2/day. The highest sustained productivity index per unit volume (1.9 gO_2/m^3) during the period occurred on 26-28 August, 1976. If that index is held constant (probably possible only during periods of maximum sunlight) and water level increased, the regression formula shows that a productivity index of 5.5 gO_2/day could be expected at a water level of about .82 meters below the USGS reference point.

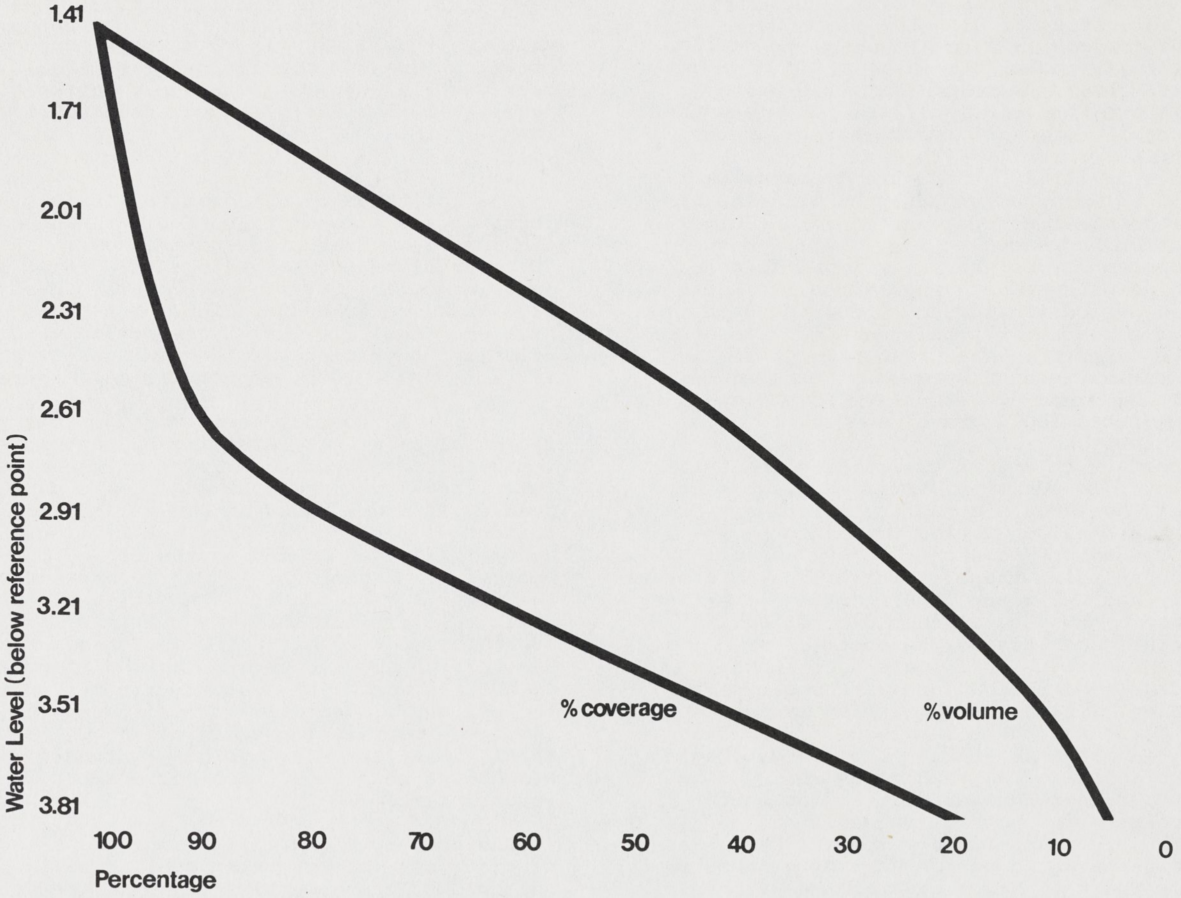

Figure 11 Percentage changes in surface area and volume of water over the natural shelf at Devils Hole as a function of water level.

An examination of the changes in surface area of Devils Hole as a function of water level (Figure 11) shows that if 0.43 m. below the copper washer is taken as 100%, .73 represents about 90% coverage, .82 represents about 85% coverage, .91 represents about 70% coverage, and 1.01 represents about 40% coverage. In estimated volumes these four levels represent 51%, 38%, 25%, and 16%, respectively. Since a fish lives in three dimensional space, the volumes represent more realistically the space available for the bulk of the important feeding and breeding activities of this species. Our data thus suggest that this species would probably fluctuate between about 200-400 individuals if water levels were maintained at about .82 m., thus providing about 38% of the volume and 85% of the surface area of the original, prepumping pool level.

As we alter our societal values, competition for use of water intensifies because one segment of society insists on retaining rights which another segment insists must shift to permit expression of other values. The importance of expressing societal values through legislation, resolution, publication, legal action, establishment of National Parks, and any other reasonable and legal manner, has been dramatically portrayed by Judge Foley's reference to such evidence as being of importance in reaching his landmark decision. Research in the National Parks is essential not alone for the intrinsic value of knowing, but also because that knowledge will frequently be essential to help guide decisions that give expression to society's values.

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logenetic association between Aulopidae and these families has been suggested on the basis of larval characters and the similar mode of anal fin support (Okiyama, 1974b, 1979b). To these can be added the peculiar structures on the chorion surface of the extremely transparent eggs, the pigmentation patterns in the newly hatched larvae, and the mode of reproduction shared by these families, characters which favor their close association.

Bathysauridae is distinguished from other families of this suborder by some trenchant differences in the peritoneal pigment sections and the mode of reproduction, while two derived states are shared by all families. The phylogenetic relationship of these families depends on whether the above mentioned differences are due to divergence. Larval stages of Bathysauridae are surely highly specialized, adapting to a prolonged pelagic life, but larval dentition described in detail by Rosen (1971) and Johnson (1974) and the character state of the axial skeleton, including the mode of anal fin support (Okiyama, 1976b) are of particular interest in showing the pattern common to Ipnopidae.

ALEPISAUROIDEI: PARALEPIDIDAE, ANOTOPTERIDAE, EVERMANNELLIDAE, OMOSUDIDAE, ALEPISAURIDAE

The similarity matrix provides certain indication of the cohesiveness of this suborder. Most remarkable is their common sharing of the derived state of character 8. Regarding the peritoneal pigment sections dividing five families into two groups, some comments are warranted for Alepisauridae. As discussed by Johnson (1982), this character state is very tentatively defined due to the inadequate state of available material. Even so, a distinct family pair of Alepisauridae and Omosudidae can be readily separated from the remaining families by the many derived character states shared by them. Although the possibility of their convergence cannot be fully rejected in view of the clear contrast in the ontogenetic aspects of the pectoral fins, the close similarity between *Alepisaurus ferox* and *Omosudis lowei* (tropical western Pacific specimen) (see my Myctophiformes: Development, Fig. 112B, E, F, this volume), in head armature and pigment pattern is extremely striking.

An association between the Anotopteridae and Paralepididae, particularly the more elongated paralepidids such as *Stemonosudis* and *Macroparalepis* (Rofen, 1966a, c), can be seen from the larval standpoint. In addition to their shared derived character states (character 7 and 8), a fleshy projection on the lower jaw tip peculiar to Anotopteridae and *Stemonosudis macrura*, and the similar larval dentition (huge canines) may substantiate the above association. Their disagreement in the character of the peritoneal pigment sections is probably associated with the odd systematic position of Anotopteridae lying at "an extreme specialized end-point of the paralepidid line" (Rofen, 1966a, c).

On the basis of the larval characters, two subfamilies of Paralepididae are well separated. As compared with the relative constancy of conservative characters in larval Paralepidiinae, the many derived character states of larval Sudinae are too specialized to be consistent with the accepted subfamilial level. The latter may be an earlier offshoot preceding the remarkable paralepidine radiation. The complete lack of intermediate forms between them offer strong support for this suggestion.

As in Scopelarchidae (Johnson, 1974b), the systematics of Evermannelidae were studied in detail using a large character suite, including larval aspects (Johnson, 1982). So far as the present analysis is concerned, this family seems variously associated with families of Alepisauroidei such as Paralepididae, Alepisauridae and Omosudidae, besides Scopelarchidae. It is of interest that limited character states shared by Evermannellidae and Alepisauridae are restricted to derived ones, probably suggesting their close association. Perhaps, an Evermannellidae and Scopelarchidae linkage is much more loose, if valid.

Concerning the possible three main lineages in this order, the larval evidence is less promising. However, additional larval evidence regarding developmental sequences, including osteology as well as internal morphology, would provide much more fruitful information for elucidating the phylogeny of this interesting group.

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Gadiformes: Overview

D. M. COHEN

GADIFORMES is a particularly interesting order with which to work because it encompasses a high degree of diversity that suggests the existence of several lineages, apparent convergence and reductive trends to trap the unwary, a useful fossil record that allows a consideration of the distribution in time of some important taxa and character states, and new suites of characters based on the study of ELH stages.

Although study of the classification of gadiforms dates from pre-Linnean times, there is still insufficient properly evaluated data available to derive a phyletic classification. In fact, there is not even agreement as to what should be included. Berg (1947) restricted the order to the muraenolepids, bregmacerotids, morids, and gadids (including merlucciids) and excluded the macrourids. He noted primitive and advanced characters in his gadiforms and suggested derivation from primitive fishes. Rosen and Patterson (1969) revived an expanded Gadiformes dating at least from the time of Gill, which included not only gadoids and macrouroids but also ophidioids and zoarcoids, and which they placed in a supraorder Paracanthopterygii, postulated as being, "in many ways more primitive than the acanthopterygians" and representing "a spiny-finned radiation more or less comparable morphologically with that of the Acanthopterygii"

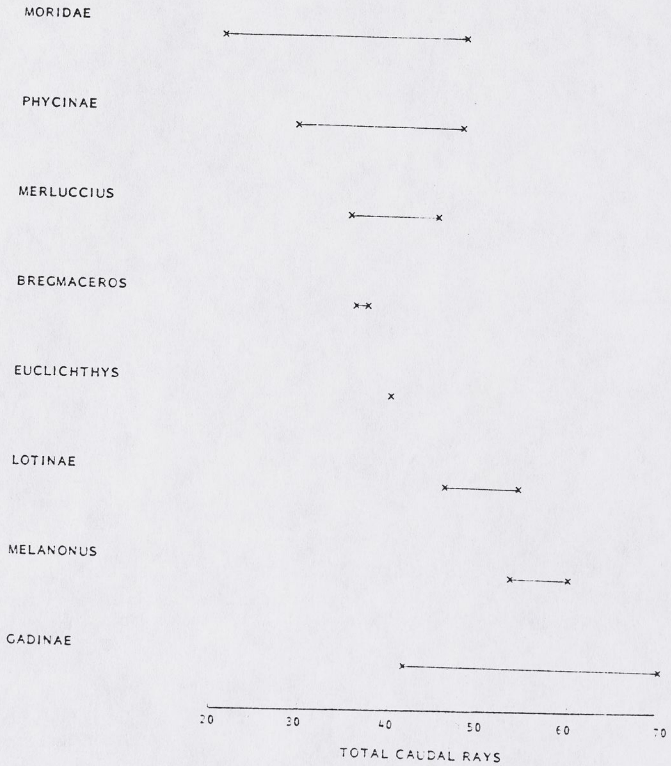

Fig. 132. Total caudal rays in eight groups of gadiform fishes. Data from Fahay and Markle (this volume) and original.

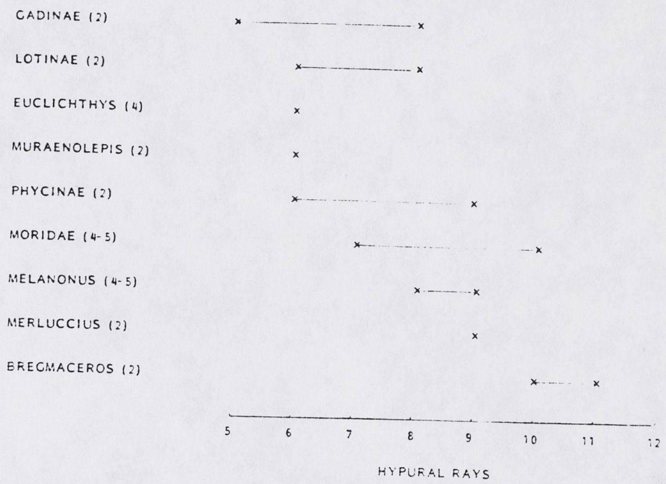

Fig. 133. Numbers of hypural bones (in parentheses) and fin rays supported by hypural bones in nine groups of gadiform fishes. Data from Fahay and Markle (this volume) and original.

and including in addition to their gadiforms the polymixoids, percopsiforms, batrachoids, lophiiforms, and gobiesocoids. Gosline (1968) analyzed the characters used in defining the expanded Gadiformes and concluded that ophidioids and zoarcoids are perciform derivatives, while gadoids are widely separate and probably close to the percopsiforms (Gosline, 1963a). Marshall and Cohen (1973), whom I follow for present purposes, restricted the Gadiformes to the gadoids and macruroids but did not consider the question of relationships. In the following brief preliminary consideration of the order, I discuss several characters, mention the groups that I think must be considered, and outline some of my ideas about the course of evolution in the gadiforms.

CHARACTERS

Several character complexes that require consideration are discussed below. Others are noted later under groups in which they occur. Additional relevant information is presented by Fahay and Markle and Dunn and Matarese in subsequent sections of this volume.

Caudal fin.—Considering the fact that well over half the known species of gadiform fishes lack the slightest vestige of a caudal fin, it is a little astonishing how much importance has been attached to the origin and homologies of the various skeletal supports and of the fin rays themselves. There is no denying, however, that when present the gadiform caudal complex is unique in several respects. Most fish groups may be characterized by a set number of branched caudal rays. Furthermore, the branched rays are generally supported by only hypurals. In gadiforms with tail fins, the number of branched caudal rays is highly variable, as is their skeletal support. *Bregmaceros* may have as few as 12 branched caudal rays, most of which are supported by hypurals, while at the upper end of the range, the lotine *Brosme* may have as many as 43 branched rays, which are supported by hypurals, epurals, and haemal and neural spines. This high degree of variation in an otherwise conservative anatomical complex lends credence to the idea of Boulenger (1902) and Regan (1903b) that the caudal fin of gadiforms is a structure newly evolved from an essentially tailless condition such as that of the macrourids or of some merlucciids. It was partly to test Regan's hypothesis that Barrington (1937) compared the development of the caudal fin of *Gadus* with that of *Pleuronectes* and concluded that, although the tail of *Gadus* was unique in several respects, it could have been derived from an ordinary homocercal tail that was less specialized than that of *Pleuronectes*. I agree with Barrington. Barrington commented also on the presence in gadids of a high number of procurrent caudal rays, which he interpreted as being far posterior dorsal and anal rays, so that the functional caudal of a cod is composed of elements of three fins, dorsal, anal, and caudal proper. This interpretation has been neither falsified nor verified by the study of early life history stages. Barrington coined the term pseudocaudal for what he took to be this kind of fin. In his lectures and during conversations with me, Ahlstrom disagreed with Barrington's explanation and its acceptance by Marshall and Cohen (1973) because procurrent rays lack pterygiophores. It is instructive to note in this respect the caudal fin structure of *Muraenolepis* (see Fig. 143 of Fahay and Markle in this volume), which has confluent vertical fins and in which the distinctive, elongate pterygiophores grade into hypurals. It is, in fact, impossible to distinguish between the last anal pterygiophore and the first hypural or parhypural. But see Fahay and Markle later in this volume.

A variety of controversial interpretations (Gosline, 1963a; Monod, 1968; Rosen and Patterson, 1969) have been advanced concerning supposed sequences of fusions and deletions of bony elements in gadiform tails. This particular use of caudal fin structure in phylogeny has yet to be proven, as few hypotheses have been verified or falsified.

For purposes of classification within the order, at least four

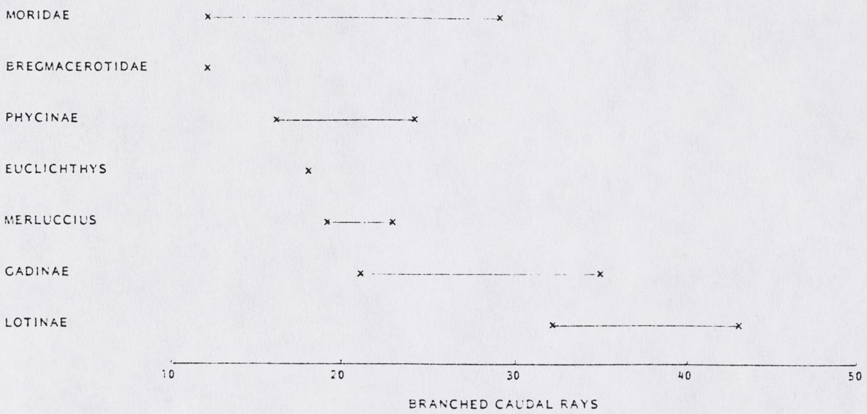

Fig. 134. Branched caudal rays in seven groups of gadiform fishes. Data from Fahay and Markle (this volume) and original.

caudal fin characters require comment. They are: 1) presence or absence of a caudal fin; 2) number of hypurals; 3) relationship between branched caudal rays, hypurals, and procurrent caudal rays; 4) presence or absence of X-Y bones.

Although vestiges of a caudal fin are sometimes found in a few macrourid species, it is essentially absent from all of them. The same is true of the merlucciid genus *Lyconus* and also *Steindachneria*. Loss of a caudal fin has certainly occurred two times and perhaps more.

The number of hypurals is a useful systematic character. There are almost always 4 or 5 in morids and *Melanonus*, and almost always 2 in gadids, *Merluccius, Bregmaceros,* and *Muraenolepis*; *Euclichthys* has 4, nearly fused to 2. I consider the lower number to be an advanced character; the study of developmental series has verified this interpretation for *Raniceps* at least (Dunn and Matarese, this volume). Certainly the loss of hypurals, whether through deletion or fusion has occurred several times in gadiforms.

The evolutionary complexity of the caudal fin in gadiforms is particularly apparent when considering the numbers of different kinds of caudal fin rays (Figs. 132–134 and Fahay and Markle, this volume, Table 76). Morids in general have caudal fins that are small and probably of reduced importance in propulsion, and which I interpret as a derived state; they also have generally fewer total rays, which Fahay and Markle (this volume) consider an ancestral state, and unbranched rays that tend to be short and contribute little to overall caudal fin size; yet, morids have 4–5 hypurals. *Melanonus* also has a weakly developed caudal fin but has 4–5 hypurals and many rays. Gadine fishes on the other hand, have well-developed caudal fins with many rays, both branched and unbranched, but have only 2 hypurals. Gadines are in general good swimmers, and one of the most active of all, *Pollachius virens,* has the most total caudal fin rays (70 in one specimen) of any gadiform fish. (Sluggish fishes like the lotines, *Brosme* and *Lota,* also have numerous caudal fin rays but have rounded caudal fins and must swim in a very different way, probably using the caudal fin as an extension of the body rather than as an oar.) Although numbers of different kinds of fin rays may prove useful in taxonomy, the relationship of branched to unbranched or total caudal fin rays is variable and has limited apparent value in the present context.

Many gadiform fishes have in their caudal fin skeletons a pair of bone splints resembling neural and haemal spines. These structures have been mentioned in the literature as accessory bones or X and Y bones and have been interpreted as modified relict pterygiophores or detached neural and haemal spines whose centra have been lost (Rosen and Patterson, 1969). I agree with Markle (1982) that the absence in any gadiform of X and Y bones is a derived character.

Dorsal and anal fins.—Gadiform fishes have 1, 2, or 3 external dorsal fins and 1 or 2 external anal fins. The number, size, and location of these fins have been used for hundreds of years to characterize groups of species. Prior to the recognition of Moridae as a distinct family (Svetovidov, 1937), convergence in this character was not recognized; most ichthyologists lumped gadids and morids with similar fin patterns.

Svetovidov (1948) assumed on functional grounds that a single dorsal and single anal is the primitive condition and arranged the gadid genera in a transition series based on increasing number of fins and the distance of their separation from each other. His hypothesis is supported by the presence in all gadiforms of a single, continuous, postanal series of pterygiophores, present even over areas that lack fin rays. Complete or partial division of the exterior fin has occurred several times, for example in the gadines, *Euclichthys, Merluccius,* and in the morid genera *Mora, Halargyreus, Lepidion, Laemonema,* and *Tripterophycis.*

Although only a few gadiforms have a single dorsal fin, the condition has a broad taxonomic distribution; examples are the gadid *Brosme,* the merlucciid *Lyconus, Melanonus,* and the macrouroidine rattails. Nearly all gadiforms have 2 or 3 dorsals, but even in those with 3, there are only two series of pterygiophores. From fewer to more dorsals would seem to be a reasonable transition series. But it certainly has occurred more than once, even within Gadidae, as Markle (1982) has demonstrated.

Pectoral radials.—Most gadiforms have five pectoral radials. *Muraenolepis* has more; *Bregmaceros* has fewer; both are interpreted as derived conditions.

First neural spine.—Many gadiforms have the first neural spine closely adpressed to the occipital crest. I take this as a derived character. *Muraenolepis* has a free spine, but it is modified by the presence of a prominent wing-shaped enlargement extending on either side of the occipital crest.

Olfactory lobes.—In his classical monograph on the Gadidae, Svetovidov (1948) discussed the position of the olfactory lobes

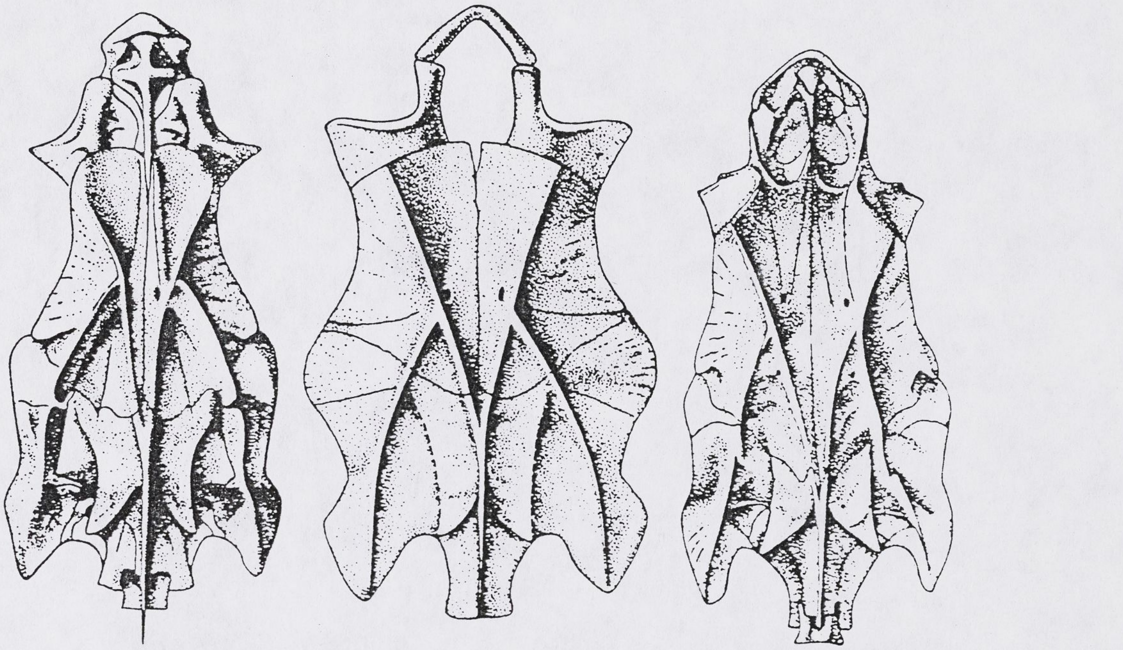

Fig. 135. Dorsal view of cranium in three genera of gadiform fishes: left, *Rhinocephalus planiceps*; center, *Palaeogadus intergerinus*; right, *Merluccius merluccius*. From Fedotov (1976).

of the brain and used their advanced position, adjacent to the nasal capsule, as his primary character for defining the Gadiformes. This is a derived character, which has been found also in cyprinids, galaxiids, and mormyrids. Svetovidov noted that the olfactory lobe is located in an intermediate position in the gadid *Raniceps*. A posterior location of the lobe was subsequently recorded in *Melanonus* and several macrourids and an intermediate location in merlucciids, *Steindachneria*, the gadid *Raniceps*, and two macrourids (Marshall and Cohen, 1973). Svetovidov (1969) pointed out the size dependent nature of this character, especially in *Merluccius* (which I have verified in *M. bilinearis* and *M. productus*). Further investigation is required, especially in species that mature at small sizes.

V-shaped crest on skull.—As long ago as 1903b Regan noted the shared presence in *Merluccius* and *Macruronus* of prominent V-shaped ridges on the frontals, which converge on the supraoccipital crest. These structures have subsequently been found in the extinct genera *Rhinocephalus* and *Palaeogadus* (Fig. 135) as well as in some fossil percopsiforms (Rosen and Patterson, 1969) and are present in varying degrees in *Lyconus* and *Steindachneria*.

Groups and Their Relationships

In this section I briefly discuss those taxonomic units that I think require consideration and explain as best possible the reasons for their placement on Fig. 136.

"Protocodus" is an unnamed species[1] from the Paleocene of Greenland (discussed by Rosen and Patterson, 1969 and Fedotov, 1976; I too have examined it), which is the oldest known non-otolith gadiform. It has a number of characters that may be interpreted as primitive for the group, including five, slender, well-separated hypurals, X-Y bones, numerous procurrent rays, and a V-shaped ridge on the frontals. It has a dorsal and anal fin configuration much like that of *Merluccius* (Rosen and Patterson, 1969).

Muraenolepis is a highly distinctive genus with four or more species. It has such primitive characters as a single anal and long-based second dorsal fin, a dermal basibranchial plate (Rosen and Patterson, 1969), the similarity of the lower hypurals to pterygiophores and to caudal fin elements, and a free first neural spine. Derived characters include 12–14 pectoral radials, a single epural, first dorsal fin a single-rayed anteriorly placed filament, vertical fins confluent around the tail, an oblique pattern of squamation, and modifications of the first neural spine. *Muraenolepis* is not obviously related to any other gadiform and appears to represent an ancient lineage.

Bregmaceros is another distinctive genus with no obvious close relatives. Like *Muraenolepis* it retains a dermal basibranchial plate, but this is a primitive character, as is possession of a uroneural and a set of X-Y bones in the tail. Derived characters include the conjunction of the first neural spine with the occipital crest, a large consolidated hypural plate supporting many branched rays, a unique lateral line system, only two pectoral radials, and a long dorsal ray on top of the head. The tropical pelagic habitat of these fishes is also different from that of any other gadiform. If fusion of the first neural spine with the occipital crest has occurred only a single time, then *Bregmaceros* must have originated after *Rhinocephalus*.

Rhinocephalus is an Eocene fossil, the skull of which has been described in some detail and compared with other gadiforms by Rosen and Patterson (1969). They mention and illustrate a

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[1] The name "Protocodus" is used as a designation of convenience and does not have formal, nomenclatural significance.

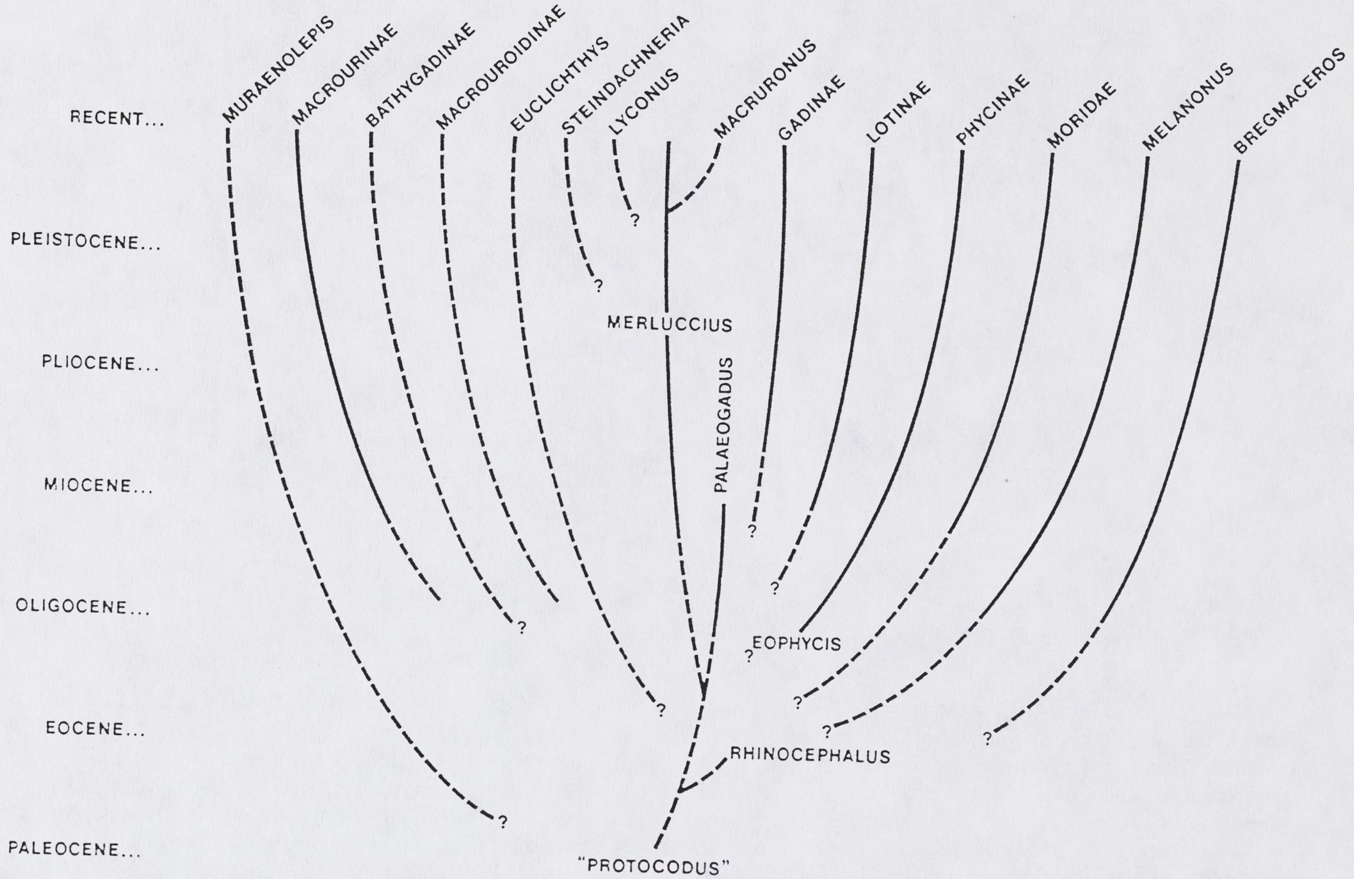

Fig. 136. Phylogenetic bush showing hypothetical inter-relationships among gadiform fishes. Beginning of solid lines based on fossils, not including otoliths or scales.

V-shaped ridge on the frontals and also lateral flanges on the rear of the skull that characterize gadines and at least some morids. They write, "The skull roof of *Rhinocephalus* shows many features common to morids, merlucciids, gadids, and macrourids . . . ." In addition, the first neural spine is free from the supraoccipital crest.

Euclichthys (Fig. 137), represented by a single South Australian and New Zealand species, was incorrectly placed in Moridae but removed by Svetovidov (1969), who pointed out some similarities to Macrouridae. *Euclichthys* can not be placed in any currently recognized family. It has a free first neural spine, which may indicate an origin prior to *Palaeogadus,* lacks an otophysic connection, has four hypurals nearly fused to two, and in two specimens has only one of the X-Y bones. As in morids, which are more specialized than macrourids and could not have given rise to them, *Euclichthys* has an asymmetrical, rather reduced caudal fin. Perhaps this curious fish is a modern representative of a macrourid progenitor.

Macrouroidinae is represented by two small genera and has been treated both as a subfamily of Macrouridae (Marshall, 1973) and a separate family (Okamura, 1970a). It has single dorsal and anal fins and a number of distinctive features in the head skeleton and may represent the most primitive tail-less macruroid.

Macrourinae-Trachyrincinae, which may well constitute two quite separate groups, has 20–25 genera and contains more than half of all gadiform species (Okamura, 1970a; Marshall, 1973). The caudal fin is absent in most, vestigial in a few; the first neural spine is free, and there is no V-shaped ridge. Eggs of the few species for which information is available have a distinctive hexagonal pattern; many species have light organs.

Bathygadinae, with two genera, differs from other macrourids in having a large, terminal mouth, dorsal rays longer than anal ones, and in a variety of other ways summarized by Okamura (1970a), who interprets most of the bathygadine characters as primitive ones. Differences in functional morphology between bathygadines as pelagic feeders and macrourines as benthic to benthopelagic feeders have been described by McLellan (1977).

Melanonus has two meso-to-bathypelagic species formerly placed in Moridae, where they do not belong as they lack an otophysic connection, have a single dorsal fin, and have lost the X-Y bones. Otherwise, they seem similar to Moridae. The first neural spine is joined to the occipital crest, suggesting an origin after *Rhinocephalus.* A separate family was proposed by Marshall (1965).

Moridae consists of 12–15 genera, some highly diverse, and all characterized by possession of an otophysic connection, 4 or 5 hypurals, X-Y bones, a joined first neural spine, and distinctive otoliths; many species have light organs. Morids probably diverged from the main *Rhinocephalus-Palaeogadus-Merluccius*

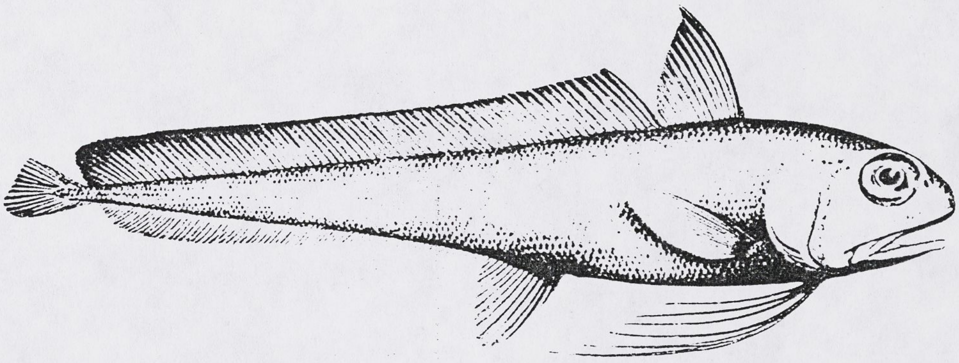

Fig. 137. *Euclichthys polynemus*, holotype. From McCulloch (1926).

line after fusion of the neural spine and at least some of their evolution is in parallel with the gadids.

Palaeogadus is a well-known Eocene fossil genus in which the V-shaped crest has been retained, but specializations include a joined first neural spine and only two hypurals. It is, in fact, very similar to modern *Merluccius*. Danil'chenko (1950), who reviewed *Palaeogadus*, believed that it gave rise independently to Lotinae and Gadinae as well as to *Merluccius*.

Phycinae, as recently modified by Markle (1982), is presently included in the family Gadidae. Fahay and Markle (this volume) would like to escort it out. An early Oligocene fossil genus, *Eophycis* (Jerzmanska, 1968) has been suggested as a precursor of *Phycis* and *Urophycis*, and probably arose independently of other gadid subfamilies, which supports Fahay and Markle's position.

Lotinae is a gadid subfamily that I mainly leave to Fahay and Markle and Dunn and Matarese. I note, however, Mujib's (1967) conclusion based on cranial osteology that Lotinae could have arisen from Merlucciinae. Lotines have no V-shaped crest but retain X-Y bones. Hypurals are two, the first neural spine is joined to the occipital crest, and there are more branched rays than in any other gadid.

Gadinae has about a dozen genera, all of which have three external dorsal and two external anal fins and a large caudal, even though there are only two hypurals. Derived characters include fused frontals, absence of X-Y bones, and a joined neural spine; Fahay and Markle and Dunn and Matarese (this volume) give more.

Merluccius, with about a dozen closely related species (Inada, 1981b), has been treated as the type of a separate family or as a subfamily of Gadidae. Primitive characters include a V-shaped ridge and X-Y bones. Advanced ones are the joined first neural spine and the reduced number of hypurals. *Merluccius* appears to be the modern representative of a lineage commencing with "Protocodus" and extending through *Rhinocephalus* and *Palaeogadus*, which it closely resembles (Rosen and Patterson, 1969).

Macruronus, which has three nominal species found in temperate waters of the southern hemisphere, is basically a *Merluccius* with a much reduced caudal fin. I mention it here because it has been referred incorrectly to Macrouridae and considered by some to be a link between that family and *Merluccius*.

Lyconus, with several pelagic oceanic species, is probably related to *Merluccius*. It lacks a caudal fin and has a single dorsal fin.

Steindachneria, is a monotypic tropical western Atlantic genus with luminescent organs, a wide separation between the anus and urogenital openings, and no caudal fin. It has been placed in Macrouridae and also considered a separate family (Marshall and Cohen, 1973). It may be closer to *Merluccius* than to any other known gadiform.

CLASSIFICATION

How best to classify gadiforms for working purposes in a way that approximates their possible phylogenetic relationships is difficult because the existence of fossils, which appears to help indicate lineages, creates logical traps for the classifier. The following arrangement, unfortunately based on gaps for some groups and on a continuum for others, is an interim suggestion for further testing.

Euclichthys is accorded family status for the first time because it can not be placed in any gadiform family. Gadidae is restricted to the gadines, and Lotidae and Phycidae are recognized at the full family level (family group names for the latter two date at least from Goode and Bean, 1896), because available evidence indicates an independent origin from *Palaeogadus* for each of the three groups. If merlucciids were reduced to subfamily rank and placed with gadines, lotines, and phycines in a more inclusive family Gadidae, then consistency would require the inclusion of at least two other well-defined apparent derivatives of the *Rhinocephalus-Palaeogadus-Merluccius* stem, Moridae and Melanonidae. In the present instance I believe that splitting is more useful than lumping.

- Suborder Muraenolepoidei
  - Family Muraenolepidae
- Suborder Bregmacerotoidei
  - Family Bregmacerotidae
- Suborder Macrouroidei
  - Family Euclichthyidae
  - Family Macrouridae
    - Subfamily Macrouroididae
    - Subfamily Trachyrincinae
    - Subfamily Macrourinae
    - Subfamily Bathygadinae
- Suborder Gadoidei

Family Merlucciidae
  Subfamily Merlucciinae (including "Protocodus," *Rhinocephalus, Palaeogadus, Merluccius, Macruronus,* and *Lyconus*)
  Subfamily Steindachneriinae
Family Gadidae
Family Lotidae
Family Phycidae
Family Moridae
Family Melanonidae

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Gadiformes: Development and Relationships

M. P. Fahay and D. F. Markle

As treated herein, the Gadiformes includes about 63 genera and 400+ species (Nelson, 1976) divided into eight fam-ies (Gosline, 1968; Marshall and Cohen, 1973); (but see Cohen, his volume). They are primarily marine with familial distri-ution "centers" as follows: Muraenolepididae—high latitudes, outhern hemisphere; Bregmacerotidae—tropical and sub-tropical, world-wide; Melanonidae—tropical and sub-tropical, world-wide; Moridae—world-wide; Macrouridae—deep sea, world-wide; Steindachneriidae—tropical W. Atlantic; Merlucciidae—mid-latitudes, both hemispheres; and Gadidae—high latitudes, northern hemisphere with minor freshwater and southern hemisphere components.

Meristic characters of genera within each family are presented in Table 72 (except that macrourid characters will be found in Table 75). Gadiforms characteristically have relatively high vertebral counts, with caudal centra outnumbering precaudal centra, usually by a wide margin. The first two centra lack ribs and parapophyses. Vertical fins have numerous rays and long bases, with posterior dorsal and anal rays separate from caudal fin rays except in *Muraenolepis* and macruronines. Pectoral fins are typically high on the body and pelvic fins typically thoracic or jugular in position. Mental barbels are found in many genera and mouth position ranges from terminal to inferior.

Present State of Knowledge and Characters of Early Life History Stages

Literature on gadiform eggs and larvae is heavily weighted towards gadids and merlucciids, within which the commercially important gadines and *Merluccius* have received most attention. Gadine larvae were among the first marine fish larvae to be described. In fact, G. O. Sar's discovery, early in the 1860's, that cod eggs and larvae were pelagic, helped initiate fisheries-oriented ichthyoplankton surveys. In addition to their commercial importance, gadines and *Merluccius* are found in shelf waters where their early stages are more accessible than those of other gadiforms which are largely residents of slope and oceanic waters.

Published descriptions of gadiform early life history stages are listed in Table 73. We especially note the seminal work on young gadids done by Johannes Schmidt in the early 1900's. Although he stressed pigment patterns over other developmental features, Schmidt was one of the first to look at several species in a systematic fashion.

In the following review, we summarize gadiform characters in brief family synopses as well as through a limited survey of the ontogeny of selected characters. Our purposes are, respectively, to point out what appear to be easily observed diagnostic early life history characters and to contribute to discussions of gadiform phylogeny.

Gadiformes.—The gut of gadiform larvae coils early in ontogeny and combined with a tapering postanal region and rounded head, contributes to an overall tadpole-like appearance. These features are, in part, a reflection of vertebral and vertical fin ray elements (Table 72) and are not diagnostic. Although it has not been documented in all families and is not always easily observed, yolk-sac and first-feeding gadiform larvae have an anus that exits laterally through the finfold rather than medially as is usual in teleost larvae. Some secondary caudal rays develop before some primary in forms with a caudal fin.

In Table 74 we summarize some developmental features of each family. A rather widespread trend is for the pelvic fin to be the earliest forming fin. There does not seem to be any character unique or diagnostic for young gadiforms. The features of body shape, anus morphology and pelvic fin development in combination with specific familial characters appear to be the most useful for initial identification. Transformation is gradual and direct with no striking changes in ontogeny.

Muraenolepididae.—A single planktonic juvenile (see discussion of planktonic juveniles below) of *Muraenolepis* sp. is shown in Fig. 138A. The distinctive first dorsal fin, composed of one or two rays, the confluent vertical fins, meristic characters (Tables 72 and 76), chin barbel, restricted gill opening and capture locality (53°48.7'S, 38°18.7'W) preclude all other teleosts and agree with characters described for *Muraenolepis* (Svetovidov, 1948). The lateral premaxillary spines (Fig. 138A) were not shown in a schematic illustration of an early *Muraenolepis* (North and White, 1982) or in larvae described by Efremenko (1983b) and are not reported for adults. It is possible that they are not found in larvae of all species of *Muraenolepis,* but for present purposes we consider them a unique and diagnostic larval specialization of the family.

[no date]

JAPANESE ANGLER

By KOSEKI SATO

PROLOGUE

ANGLING CAN BE SAID TO BE THE OLDEST AND MOST popular of all the sports on the earth. Nay, it may be even described as old as the human race, for the piscatory art was known familiarly to primitive men, although it was then practised as the indispensable means of self-preservation.

It was toward the 17th century that the art of angling began to win popularity as a hobby among high and low. In 1653, Izaak Walton wrote that world-famous work, *The Compleat Angler*, contributing thereby to the progagation and popularization of angling. Indeed, the author's well-seasoned wisdom crowning the hours of pastoral quietude beside a rustic stream seems to have developed a world-wide philosophic cult of angling out of a mere hobby. So highly has this author's work been cherished among succeeding generations of anglers, that it is reported that a new edition has been reprinted every two-and-a-half-years since its first imprint.

In Japan, *Kasenroku* (Record of Reverine Treasures), the first book on Japanese angling, was written by Unemenosho Tsugaru, a high ranking *samurai*, some 70 years after *The Compleat Angler* was published.

During the halcyon days of the Tokugawa Shogunate, when the revival of arts and literature was remarkable with the characteristic extravagance of the time, the simple hobby of angling also found its popularity increasing. To men wearied of luxuriant living and worldly this hobby, offering rural quietude and mental respite, had become an irresistible lure. The frequent mention of angling in *haiku* and *waka* (short forms of Japanese poetry) of that period reveals the popularization of angling among men of high social rank as well as among plebeians. It was during this period that angling was recognized as a hobby of somewhat nobler reputation.

Ghokakuden (Biographies of Anglers) was published early in the 18th century. This book, though written some 250 years ago, maintains even today its early reputation as the best guide book for anglers; for the valuable information contained in the work is multiple and of infinite interest even to modern anglers; it includes information on fishing grounds, characteristics of various fish, methods of angling, meteorological observations, anglers' etiquette, and so forth.

The immortality of angling has never been affected by the vicissitudes of human life. Throughout the fall of the Tokugawa dynasty in 1868 and the following Meiji Restoration of the Imperial Rule, the popularity of angling continued. *Tsurishi Katagi* (Characteristics of Anglers) which came out during that period, is worthy of note for its characteristic humor in open contradiction to the political turbulence of the day.

Neither the devastation nor the havoc wrought by the recent war discouraged the enthusiasm of anglers. Nor did the epochal change from feudalism to democracy affect the well established status of angling as every man's hobby. On week-end days, the crammed street-cars and trains convey thousands of eager hobby-anglers to their favorite fishing grounds. It is estimated that there are today in the Metropolis of Tokyo alone some 700,000 non-professional anglers.

Angling is by nature the people's hobby and everybody's sport. It is a sport healthier by far than the horse-races or the recently popularized bicycle-races. It is a kind of hobby to be enjoyed by old and young. Furthermore, viewed from the economic standpoint, it is the least expensive and most enjoyable. With a return ticket in his pocket, the angler's only need is his fishing tackle and a box of plain rice, and if necessary, a pinch or two of tobacco, and he can enjoy fresh air, sunshine and his pet hobby to his heart's content.

I dare say no housewife should have any worry over her angler-husband. She is spared the heart-rending worries suffered by her unfortunate neighbors whose husbands frequent horse-races or bicycle-races or, even worse, the disreputable *geisha*-houses. The angler's return home in the evening is the event of the day. He is invariably welcomed by his family, partly because of their curiosity and partly because of his day's absence. If his catch is too meager to enrich the evening repast, which is very often the case with the self-professed angler, that material lack can easily be compensated with the curious account of his adventure—a miraculous story in which the fish on the table can grow twice, three times in size and number, as the story goes on. In virtue, angling as a hobby has a double blessing, a blessing on the angler who grows healthy physically and mentally and another on his family who can enjoy his absence.

Angling also teaches man how to learn the true principles of democracy. On the river-bank, or beside the stream or on the sea, all the anglers realize that they are given an equal chance, and their success or failure depends upon their skill. They can complain neither of the smartness of the fish, nor the prejudicial turn in the meteorological condition. Each is taught not to be envious of his adroit neighbors. Each is made to realize that he is his own master and is responsible for his own doing.

Virtues of angling are indeed multitudinous, but let it suffice here for the author to conclude his never-ending the lotus pond), *kuri-mushi* (chest-nut worms) *tamamushi* (chrysalis in the cocoon found on the persimmon tree), young bees, various insects and catapillars found in the river, the gut extracted from fish, sweet potato, etc.

The bait is usually obtainable at the shops of fishing tackle dealers, who would know what bait should be used for the desired catch, under any seasonal conditions.

Although *kagashira* (mosquito's head) has been known since days of old, the date when flies began to be used in stream fishing is not known. The shapes, colors and size of the flies are decided by the quality of water, the conditions of fishing grounds, season, and the habits of the fish.

Flies are used mainly for fish near the surface of the water. From these flies made of bird-feathers, developed *egi* (wooden bait), which serves the purpose of floating on the face of the water much better than flies.

In catching large sea fish such as yellowtail or mackerel, flies are cast from a speed-boat, and such flies are given another name of *hikizuno* (drawn horn).

The materials for making flies are various: they are made of bird-feathers, of fish-skin or even bright colored pieces of wool yarn.

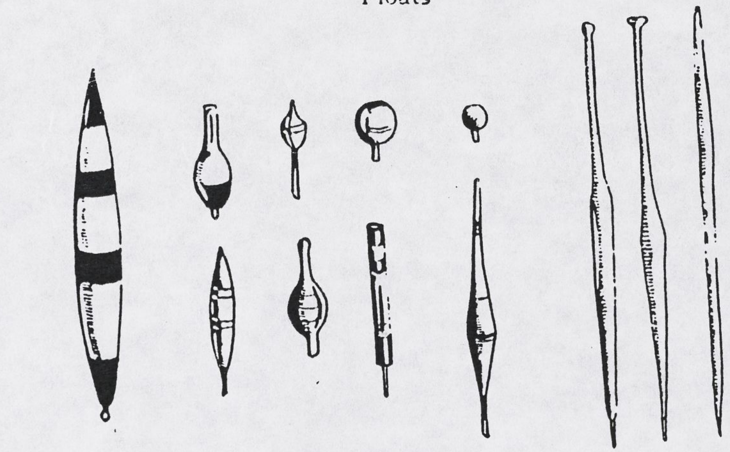
7. Fishing Tackle.

The other gadgets the angler needs on his expedition, are a basket or a pail to contain his catch, a net with a handle for the emergency use, and a box containing a pair of scisors, a knife, a whetstone, a file, a pair of tweezers, pliers, a magnifying lenze, and a reel of silk thread.

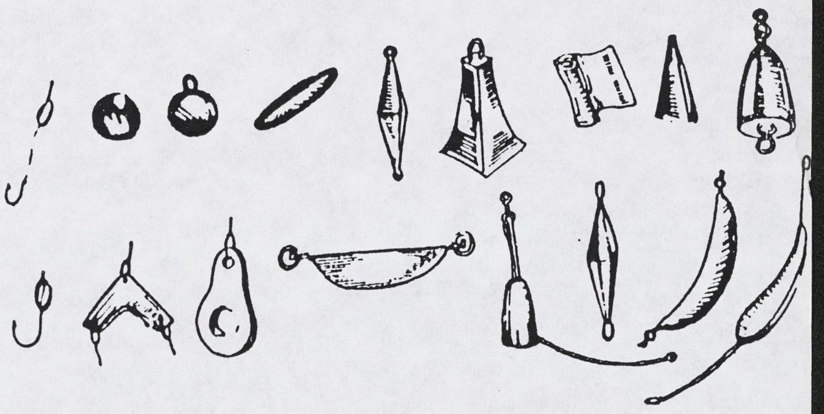
Off the angler goes to his fishing ground. But before throwing his line into the water, he must reflect on two matters; the proper arrangement of his tackle and how best he can use his own skill.

The arrangement of a fishing tackle should differ

Floats



Sinkers



Hooks