# United States Department of Agriculture FOREST SERVICE 

Rocky Mountain Region
11177 West Eighth Avenue, Box 25127
Lakewood, Colorado 30225

Dr. Robert J. Behnke
0015 J. V. K. Wagar Building
Colorado State University
Fort Collins, CO 80521

## Dear Bob:

After many disappointing delays, we are pleased, finally, to send five copies of "The Monograph of The Native Trouts of the Genus Salmo of Western North America," to you. This printing included 1,150 copies--200 for the Bureau of Land Management and 950 for the Forest Service. Paul Cuplin, Project Coordinator for the Bureau of Land Management, is now in their Washington Office--he advised their copies will be distributed mainly to their own offices from Washington. The Forest Service copies will be distributed from Denver and placed in Regional, National Forest and Ranger District offices, mainly in the West. We also are sending copies to our Forest Service Research Stations in the West and to State fish and wildlife agencies in Colorado, Wyoming, Kansas, Nebraska, and South Dakota. Our Portland, San Francisco and Denver Regional offices will have a small supply to meet outside requests for single copies.

Bob, we want to congratulate you on a job well done. We think your work will lead to improved management of trout habitat on National Forests over the entire western part of North America. Also, we believe your work may lead to enlightened trout management using subspecies having characteristics particularly adapted to specialized habitats.

Paul Cuplin asked by phone to add his congratulations to ours.


Director, Range and Wildlife Management
Enclosure (5)

DEPARTMENT OF THE INTERIOR
U.S. FISH AND WILDLIFE SERVICE

INTER-OFFICE TRANSMITTAL.
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## CHAMPOEG

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March 10, 1981

Mr. Bob Behnke
Dept. of Fishery and
Wildlife Biology
Colorado State University
Ft. Collins, CO 80523
Dear Bob:
I am returning the manuscript for the first section of your book.
I think the overall structure is good. I find one structural problem starting on page 95 and following. I think you could better make your points--special fishing regulations; restrictions on separate sections of a stream; the professional competence and administrative vigor of state Departments of Fisheries-by splitting into separate sections. Look at it and see if you agree.

I am also suggesting a number of minor stylistic changes for your consideration.
When you've had time to look this section over, I'd welcome your thoughts.
Best Regards,


Richard Abel
RA/pp
itary La-ks - Ala monusarist.
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30 Oct 1981
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## CHAMPOEG frr PRESS

P. O. Box 92 Forest Grove, Oregon 97116 (503) 357-7192

January 29, 1979

Dr. Robert Behnke
Colorado State University
Dept. of Fishery \& Wildlife Biology
Fort Collins, Colorado 80523
Dear Bob:

This letter is an effort to help work up some guidelines as to how you might recast the monograph for non-professional but articulate, intelligent and dedicated anglers.

First some background. The character of this project has become almost a crusade for the restoration of native trout populations. Bob Smith's work has grown to doing a book which will be published at about the same time as yours. The two books will compliment one another marvellously - yours the product of years of scientific study of and Bob's the product of years of angling for native trout.

This "dual" publication has it seems to Bob Wethern and me the advantage to you of permitting a direct focus on the natural history and not need, therefore, to spend effort on the angling aspects.

Now turning my suggestions on the rewrite

1. You are the authority.

Therefore, you do not have to
a. Enter into detailed analysis of the literature
b. Enter into detailed analysis of distinguishing taxonomic characteristics and locations

You can
a. simply assert what you know or believe (with suitable qualification) to be the case
b. cite only the really significant bibliographic references
c. describe the distinguishing taxonomic characteristics and location
2. You cannot underestimate the ignorance of most of your readers. So explain complicated natural history conceptions in simple language. Your readers will be intelligent and want to understand complicated concepts but they haven't the language background to deal with them in the way your scientific reader can.
3. I believe the orientation of the book should be to the evolutionary adeptation of trout to the various environments in which they are found and the wide range both geographically but also in terms of environment (cold stream and hot streams) and behavior (predation, etc.)
4. I think the table of contents might look something like this

Intro: Reasons for writing the book
a. the biologically interesting history of trout
b. value of native trout

Chap. 1 Probable Evolutionary History of Native Trout
a. Effects of climatic and geological processes on Western Watersheds
b. The various species of fish evolved
c. Interbreeding of Native populations
d. Systematic Account of Native Trout

Chap. 2 Biology of Trout
Chap. 3 Effect of Transplanting Non Native Trout
a. Hybridization
b. Effects of Hybridization
c. Systematics of Hybrid Trout

Chap. 4 Trout Habitat
a. Natives
b. Hybrids

Chap. 5 How to Reestab1ish Native Trout Populations
a. Special Regulations
b. Elimination of competing hybrids
c. Long term advantages of reestablishing Native Trout populations

After you have had an opportunity to reflect on this I'd be grateful for your thoughts.

If you can't complete the rewrite by July don't worry about it, We don't want to erode the quality of your work by meeting deadlines.

Best regards,


Richard Abel
RA:pb


Dr. Robert Behnke Colorado State University Dept. of Fishery \& Wildife Biology Fort Collins, Colorado 80523

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January 30, 1979

Robert Behnke
Colorado State University
Dept. of Fishery \& Wildlife Biology
Fort Collins, Colorado 80523
Dear Bob:

Thank you for your letter of 22 January.
Your schedule sounds very tight indeed. Could you after reflecting on my suggestions for the angler's book and your views thereon let me know how you think your schedule looks.

In talking with Bob Smith we have concluded that fairly constant checking between you and him would be desirable so that the two books compliment each other yet can stand on their own legs. Bob and $I$, obviously, in working with both your manuscripts will make every endeavor to facilatate this outcome.

Your comments on Schweibert's book is very interesting and useful.
Best regards,


Richard Abe1

RA: pb

PREFACE
I can distinctly recall a great fascination for fishes, particularly trout, from my first recollections of early childhood. Perhaps the forbidden fruit aspect of my first familiarity with fishes played a strong role in establishing a life-long desire to continually learn more about fish. As a small child, my mother had strictly forbidden me to go alone to an old mill pond on the Rippowam River near our home in Stamford, Connecticut. The lure of watching fishes in the dark waters of the pond was too great to resist. The memories of awe and mystery as I fantasized visions of what the world of fishes was like in the depths of the forbidden waters are still clearly retained.

My formal studies on trout began in 1957. After graduation from the University of Connecticut, I enrolled as a graduate student at the University of California, Berkeley, where I became a research assistant to the late Paul R. Needham. Almost immediately upon my arrival in Berkeley, Neeham and I departed on a trip through the western states, Canada, and Alaska to collect specimens of native trout for a study on the native trouts of western North America. Most of our scientific collections were made by fly fishing. We found this mode of collecting a much more acceptable way to take such beautiful specimens than by the use of nets, electricity, or chemicals. I soon developed a reverence for trout that grew through time. They assumed much more meaning to me than mere subject matter for scientific studies.

I must acknowledge that Paul Needham greatly influenced my negative feelings toward domesticated hatchery trout. When I came to California from Connecticut, I don't believe I had ever caught a truly wild trout.

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I assumed that trout fishing was dependent on the regular stocking of hatchery fish. Needham believed that fisheries based on the stocking of catchable-size hatchery trout cheapens and debases the sport of angling. He established the University of California's Sagehen Creek research station to study wild trout and to prove that, if environmental quality is maintained, a stream could support a decent fishery based entirely on wild trout and natural reproduction.

After my exposure to wild trout biology and the wild trout environment, I became a true believer in the superior qualities of wild trout and wild trout fisheries. I also recognized that as state fish and game agencies became more burdened with expanding hatchery development, proportionately fewer funds were available for doing the basic job of managing and protecting the resources and wild trout suffered as a result. It seemed outrageously unfair to me that trade-offs were being made with water development projects by mitigating the loss of wild trout habitat with increased stocking of hatchery trout. To my mind this is comparable to trading a bottle of the finest vintage French wine for a bottle of Thunderbird.

The trout that suffered the greatest declines from environmental changes and the stocking of non-native hatchery trout has been the cuthroat trout of the interior regions of the West. To call attention to the plight of many forms of rare trout native to western North America, I put together all of the information accumulated by Neeham and me and wrote a monograph on the native trouts of western North America in 1963. However, I was not comfortable with the manuscript. There were too many gaps in our knowledge, too many gray areas on the evolution and classification of the western trouts. As is characteristic of many
scientific endeavors, the more we learned about the evulutionary relationships of the western trout, the more complex the subject became. Because of my lack of confidence in what I had written in the monograph, I withdrew it from publication after the death of Paul Needham in 1964.

I now realize that the tremendous diversity found in the native trouts of western North America that make them so frustrating for an orderly scheme of classification, are actually reflections of particular adaptations evolved in different isolated environments. As such, these remnant pockets of diversity represent a resource that can be of tremendous value to fisheries management programs. There are genetic specializations for temperature extremes, predation, utilization of certain foods, and fluctuating, unstable environments. I have found great ecological differences between subspecies of a species and even between local races of the same subspecies. Fishery scientists are now beginning to realize that these genetic based ecological differences can be of great significance for fisheries management programs.

After Needham's death, I completed my graduate studies at the University of California and continued my studies on trout and all salmonid fishes. I accumulated much new information and published many papers in scientific journals, but I did not attempt to update and revise the original monograph until 1978. At that time, under the influence of the Endangered Species Act and much popular support for an environmental ethic to preserve native plants and animals, several federal and state natural resource agencies realized they had problems in relation to understanding the classification and status of the native trouts. What trout is the native trout of a particular region? How can it be
identified? How rare is it? What factors have caused its decline and threaten extinction? These were some of the questions to be answered in a new monograph on the native trouts of western North America.

Despite the great popularity of western trouts, no modern publication provided a comprehensive treatment of their classification and status. In the late nineteenth century, David Starr Jordan, America's most eminent ichthyologist and, later, the first president of Stanford University, classified the western trouts. His classification appeared in a National Museum Bulletin, "The fishes of North America," coauthored with B. W. Evermann in 1896. In 1902 this work was condensed and rewritten for popular consumption as, "America food and game fishes," published by Doubleday, Page \& Co. Although Jordan's work with fishes is indeed monumental, his work on American trouts is badly outdated and contains numerous errors and omissions. Essentially, this frequently erroneous information and classification compiled in the nineteenth century, has been the major source of published information available to anglers and angler authors who sought to learn more about native trout. Thus, my monograph completed in 1979 was also designed to update, correct, and fill in the gaps of all previous literature on the classification and biology of western trouts. The monograph was written for the Denver regional office of the U.S. Fish and Wildlife Service. It was written in a technical format for professional biologists. The monograph does, however, contain a considerable amount of information that I believe is of interest to the serious angler. This present work is an attempt to rewrite the monograph in a more readable style for a broader audience. Hopefully, as anglers become better informed, they
will become more effective in influencing state and federal agencies to protect and enhance trout environments and become skilled in articulating demands for better fisheries management programs.

## INTRODUCTION

First, I should define the terms native trout and wild trout. Often, these two terms are used interchangeably but the difference is important. A native trout occurs in a particular region because its ancestors came there by natural means many thousands of years ago. A wild trout is any trout that occurs from natural reproduction; that is, not stocked from a hatchery. In the eastern states, the brook trout is the native trout and the introduced, non-native rainbow and brown trout may occur as wild populations. In Colorado, Wyoming, and Utah, the cutthroat trout is the only native trout, but introduced, non-native wild populations of brook, brown, and rainbow trout are now much more common than the native cuttthroat.

I should also try to define the terms species and subspecies, but must admit this is difficult to do with any precision. In general, we typically envision an animal species to be a group or groups of individuals that interbreed with each other (members of their own species) but not with members of other species. That is, a species should not hybridize with another species; or, if they do, the offspring are sterile. This insures the integrity of a species by making it impossible to exchange hereditary material with any other species. For example, a horse and a donkey can hybridize to create a mule, but the mule is sterile; it cannot reproduce itself or cross with either the horse or the donkey.

The problem with the western trouts is that they have not been evolving from each other for a sufficiently long period of time to have built up enough genetic differentiation to cause sterility when they hybridize. All of the cutthroat, rainbow, golden, Gila and Apache trouts can hybridize with each other and the offspring are fertile. This lack of sterility has
been the major reason for the virtual extinction of the Gila and Apache trouts and several interior subspecies of cutthroat trout after rainbow trout were introduced by man beyond their natural limits of distribution.

In coastal waters from northern California to southern Alaska, the coastal cutthroat trout and the rainbow trout do live together and seldom hybridize. This isolation between cutthroat trout and rainbow trout in coastal waters allows a species boundary line to be drawn between the cutthroat trout species and the rainbow trout species. This isolation, however, is not the result of sterility barriers, but is due to ecological differences influencing the two species to spawn in different areas. In interior waters, however, where rainbow trout were not native, their introduction has almost always resulted in hybridization with the native cutthroat trout and the loss of the native cutthroat except in remote, isolated parts of a river system. Thus, in most of our famous western trout streams such as the South Platte, Arkansas, Gunnison, Roaring Fork, and Frying Pan rivers in Colorado, the Henrys Fork of Idaho, the Madison, Gallatin, and Firehole rivers of Montana, the Truckee River in Nevada, the native cutthroat trout is gone and the fisheries in these rivers are based on non-native trouts.

The close relationships between all of the native western trouts and the lack of sterility barriers to insure the integrity of a species, makes the recognition of a species less than clear-cut. It is difficult to define species of western trouts. They do not conform to our generalized concept of what animal species should be.

When a species consists of geographical races, these races are often recognized as subspecies. Thus, the cutthroat trout species is divided into
about 15 subspecies. All of the parts (subspecies) make up the whole (the species).

This work is devoted to the native trouts of western North America. The overwhelming majority of the various forms of native western trout can be classified with either the rainbow trout species or with the cutthroat trout species; however, some little known trout of restricted distribution such as the Gila trout of New Mexico, the Apache trout of Arizona, and the Mexican golden trout have some similarities and some differences with both rainbow and cutthroat trouts. Presently they are classified as separate species. The geological and climatic changes during the last glacial period from about 10,000 to about 75,000 years ago, played a major role in determining the distribution and some of the special adaptations of western trouts. During cooler, we.tter periods, large lakes formed in the present arid regions of the western United States. About 12,000 to 15,000 years ago a lake the size of Lake Erie occurred in the Lahontan basin of Nevada and a lake the size of Lake Michigan was present in the Bonneville basin of Utah. The site of Salt Lake City was under 700 feet of water. Much of Interstate 80 in Utah and Nevada rests on the bottom of ancient Lake Bonneville and Lake Lahontan. Giant cutthroat trout evolved in these ancient lakes to specialize as predators on the abundant populations of forage fishes. These special adaptations evolved in ancient lakes made these cutthroat trout ill-adapted for life in small streams after the ancient lakes declined to present conditions about 8000 years ago. They persisted, however, in abundance until man began to modify the environment from grazing, logging, mining, and irrigation projects and non-native trouts were introduced. Today, the native
cutthroat trout of the Lahontan and Bonneville basins are virtually gone; only a few remnant populations remain.

The past 100 years of man's impact on western waters has had a far greater effect on the rearrangement of the fish fauna than did the previous million years of evolution, geological, and climatic changes. The interior subspecies of cutthroat trout are quite rare and some are probably extinct. The greatest concentration of any interior form of cutthroat trout still persisting in their native environment without non-native trouts occurs in Yellowstone Lake and the Yellowstone River in Yellowstone National Park. Thus, unless anglers have fished for these Yellowstone cutthroat trout, it is likely that they have never seen a pure, native, interior cutthroat trout. The typical connotation of fishing for native cutthroat trout in high elevation, Rocky Mountain lakes is not quite authentic. Virtually all of these high mountain lakes occur above barrier falls and no fish were native to them. Few have suitable inlet or outlet streams for trout reproduction so they are maintained by regular plants of hatchery trout from plane or helicopter. In the past, the sources of cutthroat trout for hatchery propagation mostly consisted of various. hybrid combinations and did not represent pure populations of a state's native cutthroat trout. In recent years, there have been hopeful signs of change as some state fish and game agencies have developed management and propagation programs for their native trout. Montana now maintains separate hatchery programs for the "westslope" cutthroat trout subspecies and the Yellowstone cutthroat trout subspecies to stock mountain lakes in the various drainage basins with the correct native subspecies. Wyoming has more subspecies of a native cutthroat trout (6) than any other state.

The Wyoming Game and Fish Department is establishing brood stocks for several of their native subspecies in an attempt to increase their abundance and provide anglers an opportunity to fish for rare and beautiful native trout that most had never realized existed.

The points that I emphasize in talks at professional fishery meetings and stress in my publications, is that the preservation of the remnants of diversity still left of our native trouts has some real value beyond that of a herd of bison in a National Park. The evolutionary programming under diverse environmental conditions has endowed many of these trouts with a hereditary heritage that can be of immense practical value for fisheries management, particularly as alternatives to domesticated hatchery rainbow trout. I have caught desert basin redband trout on flies in water of $83^{\circ} \mathrm{F}$. They not only were in excellent condition and feeding at such a temperature but fought vigorously when hooked -- most trout would be expected to roll over dead under such conditions. I also found this same form of redband trout in a warm, silted reservoir with hoardes of large chubs. From casual observation, I found it difficult to believe that any trout could live in this particular reservoir in the southern Oregon desert country. The native redband trout not only lived, but flourished under this harsh environmental regime. It preyed on the chubs (just as it did thousands of years before, when an ancient lake filled this basin) and averaged about 4 pounds in weight after two years in the reservoir. Such observations suggest to me an alternative to the common fish management practice of chemical treatment of lakes and reservoirs to remove "rough" fish and restocking with domesticated hatchery rainbow trout every few years. Could we turn a "rough" fish problem into
a forage fish asset by the use of specially-adapted predatory forms of native trout?

The cutthroat trout can be more readily and consistently caught on flies and lures than any other trout species. This makes cutthroat trout extremely vulnerable to overexploitation by angling, but it also makes the cutthroat trout the species that will give the best results from special regulations designed to recycle all or most of the catch -- they can be caught again and again. This is why the catch-and-release regulations on the Yellowstone River, below Yellowstone Lake has resulted in such an excellent, high catch rate fishery. In the Madison River in Yellowstone Park, however, special protective regulations have done nothing to really influence the brown trout population -- the brown trout is much more resistant to angler harvest. I estimate that it would take at least 20 times the fishing pressure to exploit brown trout in the same proportion as cutthroat trout.

The various subspecies of cutthroat trout are not only beautiful trout that can reach a large size, they are the best species for special regulations fisheries. This attribute alone is a very practical reason why the trend toward extinction of many interior subspecies of cutthroat trout must be reversed.

Many more examples of the evolutionary adaptations of native western trouts that have application to fisheries management will be given in the accounts of each species and subspecies. I believe a convincing case can be made that fishery agencies should devote more time and funds to managing and utilizing the various forms of native trout in their management programs as alternatives to an overwhelming reliance on the domesticated hatchery rainbow trout.

GENERAL BIOLOGY
There is such similarity among all trouts in their structure, way of life, and environmental preferences, that although this work is devoted to the native trouts of western North America, much of the following discussion is applicable to trout in general. However, I would emphasize there are dangers for gross misinterpretation when going from the general to the specific and vice versa. Different evolutionary backgrounds of different groups of trout may result in very different life history adaptations. And these life history and ecological differences may not be related to differences between species or subspecies. To illustrate this point, I will elaborate on two trout mentioned in the introduction -the Bonneville basin cutthroat trout and the redband trout (an interior relative of the rainbow trout) native to the hot, arid regions of northern Nevada and southern Oregon. About 30,000 years ago the Bear River changed its course. The Bear River lost its connection to the Snake River and became a tributary to ancient Lake Bonneville, bringing the cutthroat trout into the basin. At maximum level, Lake Bonneville was about the size of present day Lake Michigan. It covered much of Utah. Great Salt Lake is the remnant of Lake Bonneville.

During the existence of Lake Bonneville the Bear River remained a large river drainage. Thus, the selective pressures of evolution divided the ancestral cutthroat trout of the Bonneville basin into two, basic ecological types -- one specialized to flourish in the great lake and one specialized to thrive in the river environments of the Bear River drainage. The length of evolutionary time was not great enough to result in clear-cut differences in the structure and appearance of the lake adapted and stream
adapted forms so all of the cutthroat trout native to the Bonneville basin are classified as one subspecies (Salmo clarki utah). The evolutionary heritage of the two forms resulted in pronounced ecological differences, however, as can be observed from their present status. The trout specializing to live in the great lake acquired ecological adaptations that made it ill-adapted to the stream environments left in the Bonneville basin after the desiccation of Lake Bonneville. They were highly vulnerable to displacement by non-native trouts and have been almost completely eliminated and replaced by non-native trouts stocked in the basin during the past 100 years. On the other hand, the cutthroat trout native to the Bear River drainage long specialized to cope with the harsh and fluctuating environments of desert basin streams. In several areas of the drainage the native cutthroat trout is still the dominant species. In 1976 I surveyed the Thomas Fork and Smith Fork of the Bear River drainage near Cokeville, Wyoming. The streams here are characteristic of the foothill region. They are turbid with heavy sediment loads. The aquatic environments appear, at best, marginal for trout. A person with a general knowledge of trout biology would predict that only brown trout could likely maintain populations in the Thomas Fork and Smith Fork rivers. Yet, I found the native cutthroat trout to be completely dominant in all sections sampled. Brown trout were restricted to two small, clear tributary streams. This situation was startling to me and would be inexplicable without an understanding of evolutionary selective pressures that had been at work for many thousands of years to make the Bear River cutthroat trout so highly adapted to a harsh environmental regime. Yet the Bear River cutthroat trout belongs to the same subspecies that disappeared so rapidly from the
rest of the Bonneville basin after non-native trouts were introduced. The subtle hereditary differences cannot be quantified or measured, but the reality of these differences are clearly expressed in the response of the two forms of Bonneville trout in relation to their resistance to being replaced by non-native trouts.

In relation to temperature tolerance of trout (brook, brown, rainbow and cutthroat trouts), numerous experiments have demonstrated the obvious -trout are cold-water fish; they come under stress when water temperatures rise above about $70^{\circ} \mathrm{F}$. With gradual increases in temperature, loss of equialibrium and death occurs at about $83^{\circ}$ F. Having this knowledge, I must admit that I was flabbergasted to find the native redband trout in an intermittant desert stream in northern Nevada, thriving in water of $83^{\circ}$. I proceeded to catch several on flies. They not only were actively feeding at this temperature, but they fought vigorously when hooked, indicating a considerable amount of reserve energy at a temperature lethal to most trouts. The explanation for this "exception-to-the-rule" is that the redband trout has been evolving in the waters of the hot, arid region of northern Nevada and southern Oregon for thousands of years. They had to adapt to these conditions or they would not be there. A practical aspect of my long campaign to preserve the remaining genetic or hereditary diversity of the native western trouts concerns the preservation of these "exception-to-the-rules" of trout biology.

This degree of differentiation between groups within a single species makes it difficult to accurately define the temperature limits, the feeding preference, the niche, etc. of the species as a whole. The manifestation of intraspecific diversity of hereditary differences between groups of the
same species, can be illustrated with a species of grape, Vitus vinifera. Virtually all wine made from grapes, the reds, the whites, generics and varietals, the finest and the poorest, are made from varieties of this single species.

Habitat, Niche, and Environment
Experienced anglers have a good understanding of trout habitat even if they do not think of it in technical terms. Experienced anglers do not cast a stream randomly. They know that trout are not randomly and equally distributed in all areas of a stream. Certain combinations of flow velocity, depth, and cover create areas when trout tend to aggregate. The physical factors of the environment that determine where a species lives is its habitat. The concept of niche concerns the role of the species in its community. It is the interaction of a species with its environment. A somewhat oversimplified, but practical, definition is that habitat is the address of the species and the niche its occupation or profession.

The environment encompasses all of the physical, chemical, and biological attributes. Thus, a stream environment includes water quality, flow and temperature regime, the substrate and channel morphology and all of the plants and animals living in or associated with the stream. The environment determines the fullness of expression of the abundance of the species.

In most streams, trout abundance is limited by habitat more so than by food. This limitation on abundance can be the result of limited spawning habitat (a situation almost never encountered in streams not modified by man), limited habitat for juvenile rearing (lack of low velocity areas with good protective cover), or, most frequently, by limited adult habitat. The preferred habitat (or microhabitat) of trout where they spend most of
their time, are the areas where experienced anglers concentrate their fishing. There is adequate depth (a foot or more), cover in the form of boulders, logs, or overhanging bank, and an area of low velocity water, usually adjacent to higher velocity flows. Trout will not expend energy needlessly fighting the current. Thus, their resting areas will be in protected sections of the stream within pockets of low velocity flow. Because most of their food is typically supplied by drifting invertebrates carried in the current, the best resting areas are under or immediately next to the main current flow so that feeding can be carried out with a minimum expenditure of energy. Because trout are territorial, the largest, most dominant trout will be established in the most optimum habitats and smaller trout must settle for second or third class accommodations. The basis for stream improvement structures to increase trout abundance (and average size) is to create more optimum habitat sites in a section of a stream. There are numerous examples where trout abundance and average size have been increased due to stream improvement measures creating new habitats. It can be assumed that the favorable response of the trout population in these cases was due to expanding the optimum habitat and not to any increase in the food supply because the structures have little or no effect on the food supply, they merely provide a site where the trout can more readily obtain food with minimum effort.

Recently there has been considerable publicity given to the study of brown trout in Spruce Creek in Pennsylvania. It is claimed that most of the trout do not seek cover, but actively feed during the day in open, relatively shallow water, contrary to popular beliefs on brown trout. Although I have never seen Spruce Creek, I doubt that anything truly revolutionary is being discovered that is not explainable on the basis of present knowledge.

Perhaps I should not cast my opinions on a stream I am not familiar with, but my interpretation of the situation is that the research section of the stream is closed to anglers and there are probably no other predators to disturb the trout in Spruce Creek. The amount of optimum habitat (first class accommodations) in the form of deeper water with adequate cover (undercut banks) is probably limited and fully occupied by the larger, dominant trout. The smaller, subdominant trout are forced to find less optimum habitat (second and third class accommodations) in sites where boulders create resting sites in the open part of the stream. The extremely slow growth rate of the Spruce Creek brown trout support my contention that optimum habitat is lacking. More energy and time must be expended in the less optimum sites to obtain maintenance rations with little surplus for growth.

The niche is a more elusive concept. It can be better visualized when two or more species of trout live together in a river. The fact that two or more species live together indicates that they must have different niches -- if the niches are identical then only one species would be there. There is broad overlap between the niches of different trout species, however, and this explains why one species can oust another. For example, warmer water temperatures have a less negative impact on the niche of brown and rainbow trouts than they do on brook and cutthroat trouts. Thus, in the larger, warmer streams, brown and rainbow trouts have replaced native brook trout in the East and native cutthroat trout in the West. If two or more species live together the environment must be sufficiently diverse to provide the requirements so that the subtle niche distinctions can be expressed. This is why larger rivers with greater environmental
diversity are more likely to support more than one species of trout than small streams.

There are many river drainages in the Rocky Mountains similar to the Poudre River that runs through Fort Collins, Colorado. Four species of trout occur in the drainage and each species is dominant in a certain zone. In the headwaters above 10,000 feet, the cutthroat trout (not strictly the pure native greenback cutthroat, but a fish predominantly of cutthroat ancestry) is dominant, giving way to the brook trout below 10,000 feet. At around 9000 feet the rainbow trout becomes dominant with the brown trout gaining the upper hand below about 7000 feet elevation. Because there are no barriers separating the species, this zonation is due to the environment favoring the niche of one species over the others in the respective zones. The end result is clearly observable but to explain how this is accomplished by the quantification of various aspects of the niche and the environment is complex and not a simple matter. It would seem that temperature is a dominant factor in this case governing species distribution. Other environmental aspects also play a role. In areas where both rainbow and brown trout occur, the rainbow is dominant in the open river channel (among boulders breaking up current velocity) and the brown trout is dominant in the deeper, slower water along the banks. This illustrates the ecological concept of the "realized" and "potential" niche and indicates a management strategy to increase total trout production. The potential niche of the rainbow trout would include the bank area if the brown trout were not there and the potential niche of the brown trout would include the open river channel if the rainbow trout was not there. The interaction of the two species living together, contracts their potential niches into their realized
niches. It follows that if two or more species of trout can live together in the same environment, the total production of all trout species will be greater than if only one species was involved.

The application of this type of ecological theory to modern fisheries management would be mainly restricted to lakes stocked with trout. By introducing two or more species (or even subspecies) with different niches, the environmental resources are more fully utilized. Several years ago my graduate students and I conducted experiments in Colorado, Utah, and Montana in lakes stocked with different subspecies of cutthroat trout and with cutthroat, rainbow and brook trout. We found that even subspecies of cutthroat trout expressed different feeding habits when living together (that is, they have niche distinctions). Besides the indication of greater total production, we found that angling appeared improved in lakes with more than one form of trout because the different feeding specializations resulted in the more frequent encounters between the angler and one or the other form of trouts.

An interesting question is: Given ideal environmental conditions, what is the maximum biomass of trout a stream can naturally support? This is a very practical question because fishery agencies must come to grasp with various aspects of this question when they make recommendations designed to maximize trout production in a river that will be impacted from a project such as a dam. How much of a decrease or increase in production can be expected if a certain new flow and temperature regime and habitat modifications occur?

Allen Binns Habitat Biologist with the Wyoming Game and Fish Department, has been been going around the state for several years measuring trout
biomass in many different streams and trying to correlate the biomass with several enviornmental factors. What components of the environment are most important for determining the abundance of trout? According to Binns' data, the most important factor is the degree of annual variation in stream flow. The best trout streams have the least variation between high flows and low flows. There is still abundant flows maintaining optimum habitat during the "low" flow period. Other components contributing to the "ideal" trout stream include nutrient level as measured by nitrate nitrogen. The waters of the best streams found by Binns have .15 to .25 parts per million of nitrate nitrogen (excessive levels from pollution are a case of too much of a good thing). The nutrient level, in turn, is related to food abundance -- the best streams are characterized by more than 5000 invertebrate organisms per square meter. Protective cover is important and this often includes well developed stands of submerged aquatic vegetation in the best trout streams. The stream banks are stable, not eroding, in the best streams and summer water temperatures ideally range between $55^{\circ}$ to $65^{\circ} \mathrm{F}$.

As might be expected, if the ideal trout stream could be created, it would resemble a spring-fed meandering meadow type of stream, with relatively constant flows and temperatures. It must be remembered that trout abundance and biomass fluctuates from year to year and from spring to fall. Typically, maximum biomass is attained in the fall of the year and due to overwinter mortality and loss of weight of surviving fish, the minimum biomass is usually found in late winter-early spring. Thus, a static figure of biomass measured at any one point in time only documents a point of fluctuating population dynamics.

Typically, trout populations are estimated from electrofishing, using mark-and-recapture techniques for increased accuracy. In large deep rivers, the effectiveness of electrofishing is limited and the population might be sampled with cyanide pellets which immobilizes the fish.

Over the years much data has been accumulated on trout populations all over the world. For comparative purposes, biomass estimates must be converted to weight per unit area, such as pounds per acre (for every mile of stream, eight feet of width equals one acre). Trout streams generally considered as fair to good angling waters typically range from 50 to 100 pounds of trout per surface acre of stream. Good to excellent reputations are characterized by 100 to 200 pounds per acre. Some "super star" streams hold more than 500 pounds per acre. In Pennsylvania, the limestone streams are highly productive. Trout biomass has been measured at 580 pounds per acre in Big Spring Creek and at 714 pounds per acre in Falling Spring Branch. Estimates in the South Platte River just west of Denver, Colorado indicate 700 to 800 pounds of rainbow and brown trout per acre in the best sections. This fantastic assemblage of trout in the South Platte River is dependent on regulated flows from the city's reservoirs upstream. In years when flows are adequate to good (particularly winter flows) the population increases. The South Platte trout fishery illustrates the significance for the negotiation of adequate minimum flows below a dam.

When a dam is constructed, the reservoir behind the dam changes a stream environment into a lake environment with a dramatic change in habitat and the creation of new niches to be filled by new species of plants, invertebrates and fishes. Fortunately, trout species are sufficiently
generalized in their life history and ecology that if oxygen and temperature regimes are suitable, they can flourish in reservoirs. Some trouts such as lake trout and several groups of Arctic charr are so specialized for living in lakes that they are almost never found in streams.

Below a dam, the temperature and flow regimes of a river changes in a manner related to the purpose of the dam. A reservoir created primarily for irrigation and flood control will tend to flatten out the annual flow curve by storing the peak flow and releasing it later in the year. A hydropower reservoir, particularly if constructed for peaking power production, will alternately shut off stream flow and then release a torrent for a few hours each day in relation to power demands.

Most high dams are constructed to release water from the deep, cold, hypolimnion zone in the reservoir. These coldwater releases have created coldwater trout environments in areas where trout environments had never existed. The large impoundments in the Colorado River basin -- Lake Mead, Lake Powell and Flaming Gorge Reservoir -- produce large trout in the impoundments and in the tailwaters below the dams, areas where trout did not live originally because of warm summer temperatures and high turbidity.

Thus, all dams are not bad for trout, some create favorable trout environments where none had existed previously. However, it has been true that fishery values historically have received little or no consideration in the planning, construction and operation of water projects. This low priority given to fishery values in relation to any project or action that changes aquatic environments must be revised if trout fishing as we presently know it is to be maintained in the future. Realistically, there is no way that all future water projects can be blocked. We can,
however, attempt to have projects operated in such a manner that does the least harm, and, hopefully, even enhances the trout environment.

It is possible, with precise information quantifying optimum habitat for the various life history stages -- reproduction, juvenile, and adult, that flow regimes can be designed to optimize trout production in a river section subject to environmental change from a water project. It is important for every state to have some kind of minimum stream flow or stream protection law to preserve its valuable fisheries resources. Sportsmen, in general, can be much more effective in influencing favorable environmental legislation and action than they have been in the past. Perhaps they have heard statements to the effect that maintaining or enhancing the fishery environment is basic for maintaining or enhancing the fisheries, that they consider such statements as cliches accepted at face value but not truly understood. Fred Eiserman, former fisheries biologist with the Wyoming Game and Fish Department, often lamented the fact that sportsmen in his state would be highly vocal in lobbying the state legislature on such matters as limiting the numbers of non-resident hunters and fishermen, but he could not get them to turn out to support stream protection legislation. Water user and natural resource exploitation groups can be counted on to lobby against environmental protection legislation. The best Mr. Eiserman could do in Wyoming to support stream protection was an endorsement by the Woman's Garden Club.

With the low population density and abundance of trout waters in Wyoming there is still plenty of trout fishing to go around in most areas. When the trout in a stream are lost due to dams, irrigation diversions, pollution, overgrazing by livestock, etc., most anglers merely shift their
attention elsewhere without much consideration of long range future consequences. How long can the degradation of trout environment go on before most anglers become acutely aware that they are losing something very precious? In Wyoming, fishing license sales have more than doubled in the last 10 year period while much trout habitat has been lost.

The environmental changes of the past 100 years have been especially hard on the native western trouts. Wyoming had six subspecies of cutthroat trout native to the various drainages of the state. Today one subspecies is extinct in the state (the greenback trout) and the other five occur at only a fraction of their former abundance. Yet the status of native trout in Wyoming is probably better than in any other western state and the Wyoming Game and Fish Department has been a leader in restoration projects for their native trout. They could use much more active support from wild trout enthusiasts.

Better multiple use management of federal lands with higher priority given to fisheries values could result in millions of pounds of increased trout (and salmon and steelhead) production annually in the western states. I particularly emphasize this point because it is one of the few possibilities of restoring trout abundance to water where they no longer occur or occur in low numbers. About half of the land mass of the 11 western states is under federal control -- mostly under the jurisdiction of the Forest Service and the Bureau of Land Management (BLM). About 75\% of this federal land is grazed by domestic livestock. The devastating impact of past overgrazing of watersheds has resulted in thousands of miles of streams now producing no trout or producing at only a fraction of their potential carrying capacity. The negative impact of livestock on trout is
effected through destruction and modification of trout habitat -- the physical structure of the stream is changed.

The typical scenario of overgrazing is as follows. During the mid to late nineteenth century, all government land in the West was essentially open to use and exploitation by anyone without restriction. This led to the days of the "open range" when enormous herds of cattle and sheep were stocked on the public lands. Densities increased until large areas were denuded of vegetation. The livestock operator who got there "firstest with the mostest" came out ahead. There was no incentive to leave any vegetation or think of the future.

Once a watershed loses most of its vegetation, rainfall is not held in place to gradually enter a stream but begins to run over the surface of the land creating gullies which coalesce into large arroyos. The annual high and low flow regime in a stream is greatly accentuated in a denuded watershed. Peak flows are much higher and low flows are much lower. The livestock have destroyed the riparian vegetation along a stream so the stream banks lack the stability of the vegetative root system to resist the great energy contained in the peak flows. When this occurs, depending on the substrate of the stream, the stream will either trench down, and cut an arroyo or break down the banks and braid out. In both cases the result is a shallow, high velocity, silt laden flow (often intermittent during the dry season) without adequate habitat for trout. This scenario has been repeated hundreds, perhaps thousands of times in the West resulting in the complete loss or severe degradation of thousands of miles of once prime trout streams.

Most anglers are only vaguely aware that livestock grazing can be a
problem to a quality trout environment. These degraded streams are avoided. Most of the major impact from livestock grazing came long ago and no living person can remember the watershed and streams in their original condition. The common belief is that the present state of affairs is due to natural erosion. Livestock people often cite the Grand Canyon as an example of erosion that livestock played no part in. This is true, but the differences between natural erosion and accelerated erosion due to man's action must be understood. Natural erosion takes place over eons of time and the surrounding environment gradually adjusts to it. Accelerated erosion resulting from livestock overgrazing, poor timber management, road building, construction activities, and stream channelization can be catastrophic in the suddenness of environmental change. Much more than fish are lost.

Although the days of the open range may be ancient history, the negative impact on our trout waters is still with us. Livestock interests aided by western congressmen have consistently delayed and blocked large scale rehabilitation of public lands which would cause a short-term reduction in their grazing allotments. By the BLM's own estimate, $87 \%$ of the well over $100,000,000$ acres of BLM grazing lands in the western states are in less than good condition. Watersheds in less than good condition result in streams in less than good condition.

Properly managed livestock grazing can avoid stream damage and rehabilitate formerly damaged streams. Grazing systems must be developed that keep livestock from congregating along stream banks and destroying riparian vegetation. The problem centers on density and dispersal of livestock. The density must be low enough to maintain a well vegetated
watershed and livestock must be kept from congregating along streams. This problem of livestock concentration in riparian zones is particularly acute in arid and semiarid regions because that is where the only water and palatable vegetation is found by mid-summer. Much of the desert type landscape characterized by deep arroyos, cactus and sagebrush were rolling grasslands with fine trout streams coursing through them 100 years ago. Change for the better will not come rapidly as long as most of the political pressure at the local, state, and federal levels comes from the livestock interest groups. The ironic aspect is that with the present poor condition of the western public lands, they produce only $3 \%$ of the forage used in western livestock production. With proper rehabilitation, the public lands could contribute to much greater livestock production than is presently possible.

There are many other multiple use activities on federal lands that can have a negative impact on the trout environment from accelerated erosion, higher temperatures, and destruction of habitat. With timbering, mining and road building, however, there are environmental guidelines governing how the project is to be carried out to minimize negative changes in the aquatic environment. When these guidelines are violated, conservationists may register complaints and have corrective action taken. Presently, there are no workable guidelines for livestock grazing that are effective in protecting the stream environment.

Anglers without an adequate understanding of habitat, niche, and environment will typically react to a declining fishery by treatment of symptoms and not the cause. A reduction in abundance of a trout population due to accelerated erosion, channelization, etc. can not be restored by instituting catch-and-release regulations or stocking eyed eggs in boxes.

The eggs placed in boxes will be subjected to the same sediment load that eggs spawned naturally are exposed to. A recent study in a stream in North Carolina carrying a high sediment load compared survival of trout eggs deposited in a gravel bed and eggs placed in a Vibert box and deposited in the same gravel bed. Hatching was poor, but the eggs, in the Vibert box had higher mortality because the eggs were in close proximity to each other which promoted bacterial growth due to the poor water quality, A poor environment for the hatching of eggs cannot be obviated by merely putting the eggs in a box.

If dedicated anglers develop a deeper understanding of the concepts of habitat, niche, and environment, they can become much more effective in favorably influencing action and programs that affect trout waters. This deeper understanding should also add a new dimension to their angling experience.

## REPRODUCTION

For a wild trout population, spawning is the most critical period of the life cycle. The range of environmental variables are most narrow and restrictive at this beginning stage of life. The oxygen demand is greatest and tolerance of pollution and temperature extremes are least during the period of egg development and particularly soon after hatching in comparison to the later stages of the life cycle.

Most experienced anglers recognize the significance of natural reproduction but are often misled in making what appears to be a very logical assumption -- if more eggs hatch, more adults will result; therefore better angling will result if the level of reproduction can be increased. The potential fallacy here is a matter of having too much of a good thing. Trout can produce an enormous surplus of young. On average, female spawners produce about 1,000 eggs per pound of body weight. If we consider the annual reproductive potential from a section of an excellent trout stream, the figures may approximate the following: A section of stream one surface acre in area has a total of 300 pounds of trout (biomass). Of this total, 200 pounds (for example, 200 fish averaging one pound each) are sexually mature and spawn in any year. About 100,000 eggs are produced (assuming 100 pounds of females and 100 pounds of males) per acre of stream. To maintain a stable population in our hypothetical stream, only two fish must survive to maturity from each pair of spawners. This means that 998 of the eggs and offspring of each spawn of 1,000 eggs must perish before attaining sexual maturity. Natural mortality can be severe and relentless. Adding more eggs in such a situation only aggravates the problem by increasing natural mortality. The environment determines
the carrying capacity of a stream section and the carrying capacity can not be exceeded under natural conditions by hatching more eggs if surplus reproduction is already occurring.

In most trout streams not highly impacted by civilization, trout do produce a surplus of young that must be eliminated each year by natural mortality and efforts to increase the abundance of adult fish by increasing the level of reproduction would be counterproductive. I emphasize that this is generally the case in streams with good environmental quality. That is, where watersheds are well vegetated, not eroding and contributing heavy sediment loads; where dams or diversions do not severely deplete stream flow during critical periods, and where favorable temperature and oxygen regimes are maintained during egg incubation. Those streams where natural reproduction is a limiting factor (that is, where increased natural reproduction would result in more adult trout) are characterized by high sediment loads which silt up the redds and suffocate the eggs and/or highly modified flow regimes which reduces flows below lethal levels at critical periods (typically just before hatching when oxygen demand is highest). Catastrophic floods during the spawning and incubation period can virtually wipe out or severely diminish a year-class (the fish hatched in any given year). Research studies on the impacts of floods have yielded much interesting information. Although very few eggs survive a flood of the magnitude of a 1 in 100 year extreme, those eggs that do survive and hatch give rise to a year class characterized by tremendously greater growth and surviveal in comparison to normal years. This is because of the low density and reduced competition among the young fish. This phenomenon of high survival and rapid growth when natural
reproduction is suppressed indicates some potentials for fisheries management. When reproduction is "too" successful and survival of young "too" high, the population becomes stunted. There is simply not enough food to go around, growth rates are extremely slow and most of the annual production (the total elaboration of fish tissue) is lost to natural mortality and little goes into producing catchable-size fish attractive to angling. In such situations, measures to suppress reproduction would be beneficial. For many years Dwight Webster and Bill Flick of Cornell University have used "genocide" tactics to manage stunted brook trout populations in private ponds in the Adirondacks. In ponds with overabundant, stunted brook trout toxicants are sprayed around the shallows soon after the young brook trout hatch in an attempt to vitrually eliminate the new year-class.

Thus, before initiating an ambitious project to increase the level of reproduction with the ultimate aim of increasing the abundance of larger trout, it would be well advised to obtain at least strong circumstantial evidence that natural reproduction is a major limiting factor governing the population size. It must also be kept in mind that the environmental factors suppressing natural reproduction (sediment, pollution, low flows, low oxygen levels, etc.) will also be in effect on any eggs stocked (also most eggs available for planting are from domesticated hatchery trout, not wild trout). There is a challenge here to discover innovative techniques that might work to hatch eggs in unfavorable environments such as suspending boxes above the bottom instead of burying them in substrate, but the highest priority should be given to treating the cause of the problem, not the symptoms. Can the sources of accelerated erosion causing heavy sediment
loads be found and corrected? Can bypass flows at dams and diversions be modified to favor natural reproduction? In Colorado and Montana, the evidence from increased winter flow releases from dams has indicated greatly increased hatch of brown trout eggs (brown trout eggs incubate during winter) and the subsequent establishment of stronger year-classes in comparison to years of reduced flow.

Thus, it is a matter of ordering priorities when the goal is one of increasing the success of natural reproduction. There are situations where devoting some time and effort to plants of eggs in boxes could be worthwhile such as in lakes without suitable inlets or outlets (if oxygen content of the water is sufficiently high -- 8-9 parts per million) and when trying to establish trout or a new species of trout in waters where they did not occur before. With degraded environments, however, it would be much more worthwhile for a group of anglers to join the fight to correct the sources of degradation (demand better land management to reduce erosion from grazing, logging, road construction, etc; demand modified flows from dams and diversions to favor trout) than to expose more eggs to the same factors that suppress natural reproduction.

The percent hatch of eggs in a good stream environment can be high -90 to $98 \%$. The obvious wild trout fisheries management goal in relation to reproduction is to maintain optimum flow and water quality parameters that result in an environment ensuring adequate natural reproduction.

All of the native western trouts evolved as spring spawners, but the timing of spawning can vary greatly depending on water temperature. Some hatchery strains of rainbow trout have been genetically selected to spawn in the fall (but only under relatively constant temperature conditions --
when stocked into natural waters and subjected to natural seasonal variation in water temperature and day length they become spring spawners). There are even a few peculiar situations where rainbow trout and cutthroat trout spawn in the fall under natural conditions. The hot spring input into the Firehole River in Yellowstone Park results in a thermal regime of optimum water temperatures for rainbow trout spawning in the fall. Normally spring spawning trout develop their gonads almost to maturity in the fall so they are ready to spawn in rising water temperatures the following spring. This early gonad development is necessary because the low water temperature and poor food supply during the winter months does not allow for surplus energy to be used in gonadal development -- the eggs and sperm must be almost ready to go before water temperatures drop below about $40^{\circ} \mathrm{F}$ if the fish are to spawn the next spring. Because of this, spawning may occur in the fall if rainbow or cutthroat trout move into warmer water. For example, October-November spawning of rainbow trout occurs in spring-fed tributaries to the North Platte River in Nebraska and some cutthroat trout spawn in the fall in spring runs coming into the Snake River, Idaho. In both cases, fish leave the colder waters of the main river and enter warmer, spring-fed sources where spawning is initiated.

Spring spawning trout typically begin spawning activities when water temperatures exceed $40^{\circ} \mathrm{F}$. Spawning generally peaks at temperatures of $45^{\circ}$ to $50^{\circ} \mathrm{F}$. High mortality and abnormal development occurs if water temperature exceeds about $55^{\circ}$ for more than a brief time, or drops below about $36^{\circ}$ to $38^{\circ}$ for very long. Fall spawning trout (brook trout and brown trout) begin spawning activity generally when water temperature drops below $50^{\circ} \mathrm{F}$ in the fall. Peak spawning typically occurs around $45^{\circ}$ to
$48^{\circ}$. The eggs develop very slowly over the winter at temperatures close to freezing, then develop rapidly and hatch during in warming waters of late winter-early spring. In both fall spawning and spring spawning species of trout, the amount of thermal units needed for hatching is about the same. From the time of fertilization, about 600 temperature units are needed for hatching. That is, eggs incubated in water averaging $52^{\circ} \mathrm{F}$, results in 20 temperature units per day (each day the temperature averages $20^{\circ}$ above the freezing point of $32^{\circ} \mathrm{F}$ ). Thus, eggs should hatch in 30 days at $52^{\circ}$ and 60 days at $42^{\circ}$. The fry remain in the redd for another 7 to 10 days after hatching to absorb the yolk sac before striking out on their own. Species of trout and salmon have a much larger egg with more yolk than do most other fishes. This results in a long incubation period, but the young fry hatch out as minature adults, better able to survive in harsh environments than would smaller larvae. As mentioned, trout can spawn about 1,000 eggs per pound of body weight; many other fishes can produce about 100,000 eggs for more per pound of body weight. Such tiny eggs develop rapidly, hatching may occur in two or three days, but the young larvae are almost microscopic in size and can be expected to suffer enormous mortality. The different evolutionary reproductive strategy followed by trouts and salmon in comparison to most other fishes is a reflection of the different reproductive environments. A relatively large size at hatching (about one inch) is necessary for survival in a cold stream environment where food is not abundant. With fish such as carp, the young hatch out in still, warm water with an abundance of microscopic organisms for the larvae to feed on.

In the mountain regions of the west, the larger, slower streams at
lower elevations will typically have several species of minnows and suckers reproducing and living with trout (generally rainbow trout and brown trout). As one proceeds upstream in the drainage, to smaller, colder tributaries only sculpins and mountain suckers are expected to be found with trout. Finally in the uppermost headwater tributaries, trout (typically brook trout or cutthroat trout) are the only species of fish that can successfully reproduce and survive in such harsh environments.

It is a common belief among anglers and most professional biologists that rainbow and cutthroat trouts need flowing water for spawning. This is generally true, but there are instances of successful spawning on lake bottoms (as is common with brook trout). Rainbow and cutthroat trouts can and will, under some circumstances, spawn on lake bottoms. The eggs, however, will not hatch unless supplied with abundant oxygen ( $8-9 \mathrm{ppm}$ ). . 5 in red

Successful reproduction in Rocky Mountain lakes may be more prevalent than commonly believed. All stocking of hatchery trout ceased in Rocky Mountain National Park, Colorado, in 1968. Many lakes in the Park have no suitable inlets or outlets for spawning. It was assumed that the cutthroat trout populations in these lakes would disappear in a few years from lack of successful reproduction. In recent years, sampling in several of these lakes lacking flowing water spawning habitats revealed several year-classes were present -- natural reproduction has been successful. The lakes are at an elevation from about 10,000 to more than 11,000 feet. Characteristically, large boulder fields and heavy snow packs occur above the lakes and gravel bars occur on the lake bottom. Evidently the snow melt percolates through the boulder field and an upwelling of high quality, well oxygenated water comes up through the gravel beds on the lake bottom.

Under these circumstances, successful reproduction of cutthroat trout and of cutthroat $x$ rainbow hybrids has allowed the perpetuation of wild trout populations in several high elevation lakes in Rocky Mountain Park where flowing water spawning habitat doesn't exist. Conversely, some high elevation lakes in the Park with inlet streams suitable for spawning are barren of trout. I believe this can be explained by the temperature regime. The water is too cold. In some of these high elevation lakes and streams the water temperature exceeds $40^{\circ}$ only for a brief period each summer. Thus spawning may not occur before August and the developing eggs are not exposed to adequate warming (about 600 temperature units needed for hatching) to hatch before winter conditions set in.

In wild trout a period of exposure to cold water (less than $55^{\circ} \mathrm{F}$ ) is necessary for normal gonad development. For this reason, many excellent trout fisheries found in tailwaters below dams must be maintained by regular stocking. The temperature regime may be fine for good growth of trout, but without exposure to low temperature, normal gonad development does not take place and no reproduction is possible.

The age at which a trout spawns for the first time is under both environmental and hereditary control. Typically rainbow and cutthroat trout (and brown trout) first spawn in their third or fourth year of life (three or four years after the eggs from which they originated were spawned). On average, males mature sooner than females. The age statistics of first spawning might be as follows: of the males, $10 \%$ spawn for the first time in their second year, $80 \%$ in their third year, and $10 \%$ in their fourth year; of the females, $30 \%$ spawn for the first time in their third year, $60 \%$ in their fourth year, and $10 \%$ in their fifth year. Sexual maturation occurs sooner with rapid growth and is delayed by slow growth. Hereditary factors also play
a role in the determination of the age of sexual maturation. For trout evolving in a small stream environment, it is advantageous to spawn at a younger age because the growth rate is not sufficient to overcome the loss of eggs resulting from reduced numbers due to natural mortality if spawning was delayed to an older age. That is, natural selection would favor the production of the greatest number of eggs at first spawning of any year-class. For example, if the survivorship and growth curves of a population shows a $50 \%$ mortality from age 3 to age 4 and only a 10\% growth increase in that time, more eggs would be produced by more smaller fish spawning at age 3 instead of fewer larger fish spawning at age 4. If, on the other hand, growth is rapid at an older age, such as in large lakes or in the ocean, it is advantageous to delay spawning until later in life. That is why anadromous stocks of steelhead trout or trout with a long evolutionary history in large lakes do not spawn for the first time until they are 4 to 6 years old. A 10 pound female spawns about 10 times more eggs than a one pound female. Even though the abundance of a year class might be reduced by 50 to $75 \%$ by natural mortality in the two years between age 3 and age 5, a greater number of eggs would be produced by fewer 5 year old females averaging 10 times the size of the 3 year old fish.

Domesticated hatchery trout have been selectively bred for many generations to sexually mature early. The development of the gonads and spawning is an enormous burden on a fish. Mortality is generally high after spawning and this is one of the basic reasons for the relatively short life spawn of domesticated stocks of trout -- they have been selectively bred for early maturation, which, in turn, predisposes them to an early
death. In most populations, relatively few trout survive to spawn a second or third time. Where data have been recorded on spawning runs, such a steelhead run or a run out of a lake, the bulk of the fish are spawning for the first time (generally about $75-80 \%$ of the run). Fish spawning for the second time typically make up 10 to $20 \%$ of the run with 2 to $3 \%$ of the run consisting of fish spawning for the third or fourth time.

Tremendous numbers of salmonid fishes are stocked in lakes and reservoirs where natural reproduction does not occur. Typically, lakes are stocked with young fish which grow and reach catchable size the following year. Under good conditions (favorable temperature and oxygen regime, lack of predators and competitors), the stocking or lakes with fingerling size salmonids has an excellent cost-benefit ratio. For each pound of fingerlings stocked, 10 to 50 pounds may be caught by anglers during the following two or three years. There is a possibility for greatly increasing this yield if sterile fish were stocked. That is, fish that have no gonadal development so that all of the energy goes into growth. In such fish the life span would be greatly increased, perhaps doubled. It is possible to produce sterile fish by introducing certain chemical compounds into the water during egg incubation. The techniques have not yet been worked out to make large-scale production of sterile fish a practical management tool, but I believe we will see lakes being stocked with sterile trout and salmon in the not too distant future.

There is a common belief that a sexually mature trout which does not spawn and resorbs its eggs will die. This is not true. The basis for this belief probably originates in lakes stocked with hatchery trout. In lakes where the trout do not spawn, females with resorbing eggs are common, but
larger, older fish are not, leading to the assumption that they all die from egg resorption. Actually, few domesticated hatchery trout will survive much beyond their first sexual maturation -- they die if they spawn or not.

A Russian biologist published a paper in 1979 on the physiological impact of egg resorption in a species of minnow and reviewed the literature on egg resorption in 30 species of fishes. He concluded from his study that no physiological harm results from egg resorption and some benefit is likely from the nutrients of the eggs being recycled in the body. I would point out, however, that I know of no controlled experiment that compared the survival and growth of spawned-out trout with trout resorbing their sex products. Until such a study is made, precise details of the impact of egg resorption can not be given, but the resorption of eggs (and sperm) certainly is not an automatic death warrant.

Age and Growth
Both heredity and environment influence the maximum life span and maximum size of trout. Because trout are cold-blooded animals their metabolic rate is related to water temperature and this results in a relatively enormous environmental (non-hereditary) influence). It is erroneous, however, to dismiss the hereditary aspect of maximum age and growth as not of great significance. For example, the domesticated hatchery rainbow trout has been selected (hereditarily changed) for rapid growth and early sexual maturation, which, in turn, shortens the life span. Under similar conditions, most races of wild rainbow trout will attain a significantly greater maximum age than races of hatchery rainbows, and this hereditary trait is of great significance when a goal of a fishery is to produce old, large fish.

As a very general rule, in most wild populations of rainbow and cutthroat trouts a maximum age of about six or seven years is found. That is, virtually no fish in the population lives for more than seven years. There are numerous exceptions to such a generality. In high elevation waters where the annual temperature regime results in only 60 to 90 days of ice-free water and with maximum summer water temperatures of $50^{\circ} \mathrm{F}$ or less, the metabolic rate and energy expenditure of trout is low and the life span is increased.

The native cutthroat trout of Yellowstone Lake has a maximum age of about seven years in Yellowstone Lake, but I have found 11 and 12 year old Yellowstone Lake cutthroat trout in South Gap Lake, Wyoming, where they had been stocked. South Gap Lake, in the Snowy Range, lies at an elevation of more than 11,000 feet and is a "frigid" environment.

The most dramatic example of a greatly prolonged life span of trout stocked into an extremely cold environment concerns the brook trout of Bunny Lake in the Sierra Mountains of California. Brook trout from a hatchery stock, which typically lives no more than three or four years, attained a maximum known age of 24 years in Bunny Lake. Bunny Lake is an extremely cold and harsh environment with very sparse food for trout. The maximum size attained by the Bunny Lake brook trout was only about 8 to 10 inches and that was "half head." They did not accumulate sufficient energy reserves to develop their gonads for spawning until they were 10 years old or more. The extreme environment of Bunny Lake so limited the metabolism and energy expenditure of the brook trout that their maximum life span was increased by about six fold over what it would have been under more normal conditions.

At the other extreme, when I was in Iran in 1974 I visited a lake (Nur L.) stocked with rainbow trout (domesticated hatchery rainbows). Nur Lake is rich in nutrients (eutrophic), has a dense population of Gammarus (freshwater shrimp or scud), and was barren of all fish before stocked with rainbow trout. Under the conditions of an enormously abundant food supply and a relatively long growing season, the stocked rainbows grew rapidly. The largest specimens reached four pounds 14 months after stocking as two inch fingerlings and attained 10 pounds in 26 months. Despite intensive netting, no trout were ever found that had lived for more than three years. The extremely rapid growth evidently greatly curtailed the maximum life span. Although it is generally true that, all else being equal, slower growing trout will live longer than rapidly growing trout, other factors introduce complications to this simple statement.

In recent years studies of lakes with Arctic charr and brown trout revealed an interesting phenomenon. In certain lakes, most of the charr and trout exhibited "normal" growth and longevity, but a few specimens much older ( 15 to 18 years) and much larger (about 15 pounds or more) were found. Precisely why a few individuals in a population live so much longer and grow so much larger than the rest of the population is not known. However, all of the large, old individuals had one thing in common -- they became predators. The large charr canabalized their own young and the large brown trout preyed on charr. Evidently, the exploitation of a new food resource, for which the few individual predators don't have to compete with the rest of the population, can rejuvenate a trout resulting in a spurt of growth and greatly extended life span. Examples of large, old brown trout, occurring at very low density, have long been known in European lakes with Arctic charr. In Scotland, the common name "ferox" has been used to designate the large trout with a greatly extended life span and at one time they were recognized as a different species.

In Flaming Gorge Reservoir, Utah-Wyoming, the abundance of trophy-size brown trout is due to the great abundance of the Utah chub. When a trout reaches a size of about 14 to 18 inches, in Flaming Gorge, it can change from an invertebrate diet to a fish diet and its growth rate rapidly increases. With this growth spurt, it is probable that the life span is prolonged beyond what it would have been if the older individuals had to compete with younger trout for small invertebrates.

The lesson here is that for a body of water to produce both old and large trout, large food items must be present.

As will be discussed later, however, the deliberate introduction of
forage fish into a lake in hopes of increasing the growth rate and maximum size of trout can have disastrous consequences.

Fish growth is indeterminate. That is, fish have the potential to grow throughout their whole life. Because of environmental factors such as water temperature, length of growing season, abundance, availability, and size of forage organisms, the maximum size attained by trout with the same hereditary background can vary enormously.

There is also a genetic or hereditary influence on the maximum size a trout can attain. There are differences in maximum potential size between species. For example, the "world record" size for brown trout, rainbow trout, and cutthroat trout is about three times greater than for brook trout. Among subspecies of cutthroat trout, the subspecies native to the Lahontan basin of Navada and California can attain a maximum size two or three times greater than that of many other subspecies.

Even finer degrees of hereditary influence on maximum size can be observed in the native rainbow trout of Kootenay Lake, British Columbia. There are two distinct races of rainbow trout native to Kootenay Lake. One is a "normal" population which spawns at two or three years of age, lives to a maximum age of five or six years and seldom exceeds two or three pounds in weight. A race of "giant Kamloops" rainbow trout also lives in Kootenay Lake. It doesn't reach sexual maturity until it is four or five years old and may live for seven or eight years and reach a weight of 20 to 25 pounds. This race of Kootenay "Kamloops" trout was transplanted into other waters where it also exhibited excellent growth. When stocked into Lake Pend Oreille, Idaho, it found an abundant food source in the dense population of kokanee salmon which resulted in phenomenal growth.

A specimen caught in 1947 from Pend Oreille weighed 37 pounds and was only five years old. This fish was long recognized as the world record rainbow trout. The Kootenay "Kamloops" trout stocked into Jewel Lake, British Columbia reached even greater maximum weights. A specimen was once trapped during spawn taking operations that weighed 52 pounds.

Steelhead fishermen are aware that the steelhead trout of different rivers may vary considerably in average size. A difference in average size is also common between summer-run and winter-run steelhead in the same river. These differences in average and maximum size among steelhead runs has a hereditary basis, and is mainly determined by life history characteristics. The largest steelhead spend more time in the ocean and sexually mature at an older age than smaller steelhead. The Skeena River drainage near the British Columbia-Alaska border probably has the largest steelhead of any river system. The present world record rod-caught rainbow trout of 42 pounds was caught off of Bell Island, Alaska, near the Skeena River mouth. This record fish was probably derived from the Skeena system.

A variety of hereditary or genetic based life history attributes which govern age at sexual maturity, maximum life span, and predatory specializations can be found in natural populations of our native trouts. These are the traits that determine the maximum size of trout, yet they have been not only ignored, but actively selected against in the history of hatchery propagation in order to produce a cheap article.

Food and Feeding
Trout are pretty much opportunistic in their feeding habits. They feed on a wide spectrum of organisms and will generally consume what is
available and edible. These statements appear to contradict what is common knowledge among anglers, that trout can be highly "selective" in their feeding in response to fishermen's flies and lures. This feeding "selectivity" that has been frustratingly experienced by all trout fishermen and is an integral part of the mystique of trout fishing can most logically be explained by the "availability" of forage organisms.

In most streams, virtually all of the trout's food is taken in the "drift" of aquatic insect larvae in the current and of adult insects, both aquatic and terrestrial, on the surface (some low velocity streams with aquatic vegetation may have a considerable abundance of crustaceans which may form a significant part of the trout's diet). Only one or a very few species may predominate for several days in the drift or on the surface. The brain of a trout is rather primitive and its sensory systems become conditioned or programmed to feed on the available food item. Laboratory studies have shown that when trout are fed on one item such as meal worms for about a week they will not readily feed on a new item immediately. It takes a few days of exposure to the new item before the trout's sensory system becomes attuned to it and it isreadily taken. Thus, "selective" trout result when only one or two food items are available for several days. In some environmentally stable sections of a river, such as below a dam that releases a relatively constant flow and temperature regime, the invertebrate density might be high, but may consist of very few species. In such situations, the trout's diet is very limited in diversity. They become strongly conditioned to feed on only a few species of insects such as chironomid larvae. Under such circumstances, feeding is highly "selective" and only flies that match the size, shape,
and color impression of the natural food can be expected to consistently catch fish.

The same principles govern feeding in lakes; however, crustaceans (zooplankton, scuds, sowbugs, etc.) typically provide the bulk of the food consumed by trout. As a general rule, the diversity of invertebrate fauna decreases in lakes at higher elevation. In deep, high elevation lakes it is common for trout to feed on a single species of water flea (Daphnia) for long periods. I know of no way a water flea of about 1 mm (1/25 inch) can be Mintjated by an artificial. In such lakes, even the normally "dumb" cutthroat trout can appear to be just as "selective" as old brown trout in roadside waters.

As a general rule then, the more diverse the available food in size, shape, and color at any given time, the more likely are the trout to take a variety of flies and lures.

In general, rainbow and cutthroat trouts and most other species of trout and salmon feed and grow most intensively when water temperatures range bewteen $48^{\circ} \mathrm{F}$ to $68^{\circ} \mathrm{F}$. Feeding continues, if food is available, at temperatures down to the freezing point, but the metabolic rate of trout is so reduced at temperatures below about $40^{\circ} \mathrm{F}$, that a growth increase is unlikely. Typically there is a weight loss over the winter months unless there is an area in a stream or lake with temperatures of more than $40^{\circ}$ and available food. Near the freezing point of water, it takes a trout about seven days to fully digest a meal that would be digested in 24 hours at temperatures of $55^{\circ}$ to $60^{\circ}$. Despite the experimental evidence that trout feed at a much reduced rate at very low temperatures and need little food at low temperatures, many anglers find some of their fastest fishing
during the winter months, ice fishing in lakes or fly fishing in streams. This apparent contradiction that catch rates often increase as feeding intensity is drastically reduced by cold water can be explained by food availability. Food becomes difficult to find because the invertebrates move little in frigid waters. Therefore, even though the need for food is low, trout must spend more time actively seeking the sparse numbers of invertebrates that are available and this increases the chance of a feeding fish encountering the offering of an angler.

In areas where winter conditions are hard and ice and snow persist for five or six months, overwinter mortality can be high. Trout that have a high energy reserve (intensive fat deposition) have the best chance of surviving harsh winters. In streams, deep pools with good cover, such as large boulders, enhance overwinter survival of a trout population.

At the other extreme of high temperatures, trout typically continue to feed up to temperatures of about $75^{\circ} \mathrm{F}$, but at temperatures of about $70^{\circ}$ they are at a severe disadvantage in competition for food with "warm-water" fish species. Trout evolved as cold-water specialists; their sensory systems and physiology function best in colder waters. At temperatures below about $60^{\circ}$, salmonid fishes have a competitive feeding advantage over virtually all other fishes native to North America. They not only hold their own, they are the dominant, often the only species of fish found in cold, high elevation streams. When temperatures increase above $70^{\circ}$, the physiology of trout becomes stressed, its sensory systems do not function optimally, it can not find and capture food effectively. At the same time, oxygen demand increases with increased metabolism and energy expenditure.

Lower elevation ponds and lakes with marginal summer water temperatures
for trout are often the most productive trout waters known--as long as no warm-water fish species are present to compete with the trout during the critical summer months. Once the warm-adapted species of minnows, suckers, catfishes, and sunfishes become established in such waters, the formerly excellent trout fishery is ruined.

The above discussion is based largely on practical and experimental results using hatchery rainbow trout. As I have stressed, there can be great differences within a species in life history, behavioral and physiological attributes. A very significant question is: are there special temperature adaptations found in some races of native trouts that could be utilized to greatly improve trout fisheries in waters presently considered marginal or submarginal for trout due to temperature limitations? Are there "warm-adapted" trout whose physiology and sensory system continue to function well at temperatures of $75^{\circ}$ or more? Could such trout be introduced into marginal waters where domesticated hatchery trout fail and successfully compete with and prey on the nongame fishes?

I have observed the native cutthroat trout of the Humboldt River drainage, Nevada, thriving in small streams where summer water temperatures reach at least $78^{\circ}$. This same trout, gaining access from small tributary streams into Willow Creek Reservoir, a warm turbid impoundment with an abundant chub population north of Tuscarora, Nevada, grow up to seven pounds. Several plants of hatchery trout into Willow Creek Reservoir resulted in poor survival and negative growth.

In northern Nevada and southern Oregon, the redband trout evolving in this harsh, arid environment continues to feed at a temperature of $83^{\circ}$. In warm-water reservoirs (submarginal trout waters by almost any
standards) these arid lands redband trout reach a large size and evidently are an effective predator on the native chub.

We should soon be learning more about the potential of the Oregon redband trout because the Oregon Department of Fish and Wildifife has initiated a propagation program for this fish. I would express caution however against premature optimism that a new era of fisheries management is at hand. Until there is a real appreciation of the potentials that various native trouts have for fishery programs and an understanding of how the principles of evolutionary biology can be applied to these programs by the people who determine these programs at the higher administrative levels, a departure from an overwhelming reliance on the domesticated hatchery rainbow will not be likely. Until this educational process occurs, work on the practical use of native trouts will continue to receive low priority and low funding. Projects will be local and desultory without proper "before and after" type of studies necessary to obtain the data for adequate assessment of the management potential of the various races of native trouts. Informed anglers and angler organizations can play a role in speeding up this education process.

Our typical conception of a classic mountain trout stream--cold, pure, and crystal clear--is indeed a thing of beauty, but, it is also likely to be deficient in nutrients which greatly curtails the production of aquatic invertebrates. A nutrient deficient stream, poor in food production, may still, however, maintain a sizeable population of trout if the physical habitat is good. This is the result of the contribution of terrestrial invertebrates to the trout's food supply. In the summer months it is common to find $50 \%$ or more of the trout's diet in small streams to consist of food from the terrestrial environment such as grasshoppers, ants, beetles, etc. In general, the
the amount of terrestrial input is correlated with the condition of the riparian vegetation. Vigorous growth of vegetation along the stream and overhanging the stream will result in more trout food of terrestrial origin than barren stream banks. Although the main value of riparian vegetation to a trout stream is the root system which stabilizes banks, reduces erosion, and creates habitat, the foliage also can be of considerable significance by increasing the terrestrial component of the food supply.

What might be done to increase the food supply and food availability to trout? This question can be broken down into two separate components: 1. Possible ways to increase the production of organisms already there, and 2. Possible introductions of new species to fill gaps in the food web.

The simplest way to increase production of invertebrates and fishes is to increase the primary production of plants and algae. This can be done by increasing the concentration of nutrients especially nitrogen and phosphorous. The introduction of fertilizer in water has the same effect as it has on land. The danger here is that greatly increased production of organic matter can cause oxygen depletion and fish kills when the effects of respiration (oxygen used, carbon dioxide given off) exceeds the effects of photosynthesis (carbon dioxide used, oxygen given off), or when a massive die-off of vegetation occurs, using up oxygen in the process of decomposition.

A small amount of pollution enrichment, such as sewage effluent, if greatly diluted in a stream or lake so that problem levels of oxygen depletion do not occur, will result in increased fish production. The Bow River near Calgary, Alberta, is an example of an artificially enriched stream (mainly sewage) that supports an excellent trout population.

However, further enrichment or periods of prolonged low flows would likely result in severe oxygen depletion and fish-kills.

By and large, however, the idea of increasing trout production by enriching a stream or lake with sewage effluent is not particularly attractive to most anglers.

The introduction of new species of forage organisms has much greater chance of success in lakes rather than streams. This is due to the fact that the predominant invertebrate trout food in streams are insects which have an adult flying stage in their life history. This allows dispersion over a wide area. In any particular geographic area, the same species of mayflies, caddisflies, stoneflies, and Diptera are found in similar types of habitat. If a species common to one stream is not found in a neighboring stream it is because the essential habitat is lacking and transplanting the insects from one stream to another will not succeed in establishing a new population.

In lakes, the predominant trout foods are typically crustacea which do not have a flying or terrestrial stage in their life history. Because of these limitations to nonaquatic dispersal, crustaceans are not so universally distributed. This is especially true with large crustaceans such as crawfish and "opposum shrimp" (Mysis).

As a food source for trout, one of the best invertebrate animals is the freshwater shrimp or scud of the genus Gammarus. Scud utilize the lowest part of the trophic scale or food web for its own food and converts this low trophic level directly into high quality trout food. The scud also inhabits the same temperature and habitat zones as trout and are readily available prey.

Trout that feed predominantly on crustaceanis will have pink, red, or
orange flesh. This coloration is from carotene pigment with which crustaceans are richly endowed. Insects have little carotene and trout feeding exclusively on insects will have white flesh.

A note of caution must be made concerning potential harmful impacts from the introduction of forage species. A lack of knowledge on the introduced species and the role it will play in the new environment can result in reducing the production of trout or other game fishes. Such harmful effects occur when the new organism competes with trout for a common food supply, but is not consumed itself by trout in sufficient quantity to compensate for the food deficit.

Several years ago many western fish and game agencies began concerted efforts to establish the "opposum shrimp", Mysis relicta, in many large, deep lakes. The opposum shrimp is a rather large freshwater crustacean reaching about an inch in length. It occurs naturally in some lakes in the Great Lakes region and in Canada. Where it occurs, Mysis is typically an important food for lake trout. The establishment of a large crustacean such as Mysis to increase trout production in lakes seemed a very logical thing to do. Within a few years after Mysis became established in many western lakes, the fisheries for kokanee salmon and rainbow trout have been largely ruined. On the other hand, lake trout, if present, have benefitted from Mysis introductions. How is this phenomenon explained? What went wrong? The most detailed research on the impact of introduced Mysis on the aquatie ecosystem has been done at Lake Tahoe, where Mysis were stocked from 1963 to 1965. It was found that Mysis is a very effective predator on small zooplankton, particularly the crustacean orders Copepoda and Cladocera. The copepods and cladocerans ("water fleas", etc.) are
small crustaceans typically 1 to $3 \mathrm{~mm}(1 / 25$ to $1 / 8 \mathrm{in}$.$) in size, but$ they typically form the bulk of the diet for kokanee salmon and often rainbow and cutthroat trouts in lakes. Within a few years after Mysis became established in several western lakes, the copepods and cladocerans virtually disappeared. The zooplankton food supply that formerly maintained large populations of kokanee salmon and trout was lost. Why don't the trout and kokanee avidly feed on the large Mysis?

Mysis has a peculiar trait of remaining on or near the lake bottom in deep, cold water during the day, and migrating to the surface zone of the lake at night. Trout and kokanee do little if any feeding on zooplankton in the pelagic, open water zone of a lake after dark and the temperature of the water near the bottom in deep lakes (about 100 feet or more) is below the temperature preference for trout and salmon feeding. Thus, only lake trout make use of the new food supply, but the overall fishery suffers a great decline. Also the production rate of Mysis is much less than that of the smaller species of zooplankton it replaces. Mysis require 1 to 4 years to sexually mature and reproduce. Small species of zooplankton attain reproductive age in 2 or 3 weeks. Thus, the "turn over" or production of populations of small zooplankton is rapid. These populations replace themselves several times during a year. Their production rate is high-the total weight or biomass produced during the year by small zooplankton is several times greater than the biomass found at any single time. In contrast, an organism such as Mysis which reproduces or replaces its population only once per year or less, has a lower production rate and will contribute proportionately less to the total food supply of fishes. Thus, what once seemed to be a logical and well-founded attempt to increase the food supply for trout and salmon has turned into a disaster for the fisheries of several western lakes.

I would point out, however, that in relatively shallow lakes (about 40 to 50 feet maximum depth) where the bottom water temperatures do not drop below the preferred feeding temperatures of trout and salmon, the trout and salmon would probably prey intensively on Mysis to limit their population and allow for the continued existence of healthy populations of small zooplankton. Evidently this is the case in Kootenay Lake, British Columbia.

With an abundance of small zooplankton (1-2 mm size), rainbow and cutthroat trouts grow rapidly to about 12 inches and then growth is very slow unless larger food items are available. This is due to the fact that as trout grow, the gillrakers on the gill arches become more widely spaced. The gillrakers trap the small organisms that are taken in the mouth and funnel them to the esophogus for swallowing. At a size of about 12 inches, the gillrakers on most trout are spaced so that the gaps between them allow the small organisms to pass through with the respiratory current. Kokanee salmon have much more numerous and better developed gillrakers than trout for straining small zooplankton. For this reason, the introduction of kokanee salmon into a lake with rainbow or cutthroat trout where the main food supply is small zooplankton, can ruin the trout fishery. The kokanee has much superior adaptations to utilize small zooplankton than does the trout and the kokanee captures a much greater share of the common food supply.

The problem remains then of what might be done to produce larger trout in lakes where size is limited by the small size of food organisms. The introduction of forage fish once seemed like the obvious solution to this problem. After numerous excellent trout fisheries were ruined by the
introduction of "bait" or forage fish, it became clear that this is not a practical solution. The problem here lies in the fact that most of the species of minnows introduced to feed the trout eat the same invertebrate animals that trout eat, and they are better adapted to feeding on them in warmer water and in weed beds. The addition of a new link in the food chain decreases trout production because of the "conversion" factor. Energy is lost going from one trophic level to the next. For example if it takes 100 pounds of invertebrates to increase the biomass of the minnow population by 10 pounds, and 10 pounds of minnows to increase the biomass of the trout population by 1 pound, then, if all functions efficiently, 1 pound of trout is obtained from 100 pounds of invertebrates consumed by minnows. If the trout fed directly on the 100 pounds of invertebrates, their increased production would be 10 pounds or 10 times greater than that obtained by passing the invertebrates through an additional link in the food chain.

The typical outcome from the introduction of forage fish in trout lakes is that a few trout survive long enough and attain a size (typically about 14 inches) where they become effective predators on the forage fish. This results in a few trout reaching a much greater maximum size than was formerly possible without the forage fish, but the overall production of trout suffers a drastic decline.

The ideal forage fish would be one that does not compete with trout for a common food supply. That is, a fish that utilizes a food source not used by trout and in turn can be readily preyed upon by trout, thereby converting an unutilized part of the food resources into trout food. In reality there is no "ideal" forage fish. Alewives and threadfin shad
have greatly increased trout production and growth in some lakes and reservoirs, but these efficient plankton-straining fishes can severely deplete the zooplankton community. If the trout have suitable alternate food resources such as benthic invertebrates, to attain a size necessary to prey on alewives and threadfin shad, then the introduction of these species can result in increased production and growth of trout.

A large invertebrate organism that can be excellent trout forage is the crawfish. Crawfish are members of the crustacean order Decapoda. Most decapod crustacea are marine animals such as crabs, lobsters, and marine shrimps and prawns. Crawfish are essentially "freshwater lobsters." I know of several lakes where trout growth was increased after crawfish were introduced. Some species of crawfish can reduce excessive vegetation by their feeding and biological control of a vegetation problem is much preferred over chemical control. Most species of crawfish are omnivorous, feeding on a variety of living and dead plants and animals, but they do not compete with trout for the bulk of their food.

Before crawfish are stocked into a lake some consideration should be given to the best species to introduce. Different species have different life history characteristics. Some species are much more available to predation than others.

Among the various races of our native western trout, subtle feeding differences and feeding specializations have evolved. Many lakes and reservoirs have a good trout environment in terms of temperature and oxygen regimes, but have only limited trout production because the food supply is utilized by forage or "rough" fish (that is, hatchery rainbow trout stocked into such waters have poor survival and growth). Yet some of our
native trouts have evolutionary predatory adaptations to effectively prey on some of these "rough" fishes. To my mind, one of the great shortcomings of modern fisheries management and fish culture is that we have not really made much use of the potential presented by the special feeding adaptations of our native trouts.

Intraspecific feeding specializations--the differences found between races of rainbow trout and between races of cutthroat trout--are more pronounced than interspecific feeding differences between the rainbow trout as a whole and the cutthroat trout as a whole. The Eagle Lake, California rainbow trout evolved feeding specializations to prey on tui chubs. The "Kamploops" rainbow trout of Kootenay Lake and many other lakes in British Columbia, prey on kokanee salmon and other native fishes (thus it was "preadapted" to effectively utilize the abundant kokanee in Pend Oreille Lake). The desert region redband trout of southeastern Oregon evolved specializations to feed on the native chubs. The Lahontan cutthroat trout has a long evolutionary history as the top predator in the Lahontan basin.

Further experimentation on how to best make use of the evolutionary resources of our native trouts can lead to a new, enlightened era of fisheries management--and better trout fishing.

Movement and Migration
I once appeared as an expert witness in a court case. A major issue involved concerned movement of stocked rainbow trout into and out of a section closed to fishing. I convinced the judge that rainbow trout do not typically "move" very far up or down a stream, but had to admit that in certain cases rainbow trout may make long migrations. The key to this explanation is the definition of the terms. A migration is an extended and directional movement and is an integral part of the life history. Trout can not spawn in the ocean and most lakes so they must migrate to suitable spawning sites if the population is to be perpetuated. "Ordinary" movement is an every day activity covering short distances such as moving from a pool to a riffle to feed, or movement under cover when disturbed.

Resident trout in streams, once reaching a size of about six inches or more, typically in their second year of life, find a territory or microhabitat area and essentially stay put thereafter (if not driven out by a larger trout). A knowledge of trout movement (or lack or it) is an important part of fisheries management. Until the 1930's and 40's, it was common to find that state fishery laws closed headwater tributary streams to angling because it was believed that these tributaries were used as spawning and nursery areas for the trout population in the main river.

Many years of study on trout movement by marking and recapturing individuals, have shown that in most small tributaries, the trout population is self-contained. Almost all fish are born and die in the tributary without moving to the main stream. Another management tactic was to close a section of a river as a "trout sanctuary" in the belief that under protection from angling, the trout in this section would multiply and the
surplus would radiate out into the open waters. Such -a strategy sounds logical but it really doesn't work because resident stream trout do not move much. An interesting test of the sanctuary idea was made on Lawrence Creek, Wisconsin, a popular brook trout stream. A one mile section of Lawrence Creek was closed to fishing, the population of brook trout in the section enumerated and weirs placed at the upstream and downstream ends of the closed area. For five years the brook trout were counted in the closed area and movement into and out of the sanctuary recorded. More trout actually moved into the sanctuary than moved out. Yet at the end of five years of complete protection from angling there were fewer trout in the one mile closed section than were there when the area was open to angling with a rather high angler take of fish. The trout sanctuary on Lawrence Creek resulted in a significant loss of trout to the fishery.

The absence of pronounced movement in resident stream trout allows for different types of regulations to be instituted on the same stream. For example, a one or two mile section of catch-and-release regulations can be instituted between sections of a river open to statewide regulations. The trout population in the catch-and-release section will increase to carrying capacity (assuming that angler kill had held it below carrying capacity) and will not "spill over" into the adjacent sections. This lack of trout movement allows separate sections of a stream to be managed as separate entities.

In streams trout will move as far as necessary to find suitable spawning gravel for reproduction. Typically, suitable spawning areas will be found within 100 feet of the trout's territory or microhabitat and a long migration is not made. Steelhead trout in the ocean and rainbow and
cutthroat trouts in lakes, however, may make long spawning migrations.
The longest spawning migrations of steelhead were once made to the upper Columbia River in British Columbia (this run was exterminated by Grand Coulee Dam in 1939) and to the upper Snake River, near Twin Falls, Idaho (this run was eliminated by Hells Canyon Dam in 1964). These runs migrated almost 1000 miles from the ocean. It was not generally realized when the Columbia River basin dams were planned and constructed that the steelhead that spawned in the basin were not a homogeneous population, but consisted of numerous, separate races. Each race spawned in a different major tributary or a group of adjacent tributaries. Each race evolved special adaptations precisely attuned to utilize a particular segment of the Columbia River basin. Thus, a race spawning far from the ocean needs considerable time to reach the spawning grounds. They may leave the ocean and begin their migration 8 to 12 months before actual spawning occurs ("summer"-run fish). These early-run fish feed little in freshwater and must have considerable energy reserves (fat deposits) to survive for long periods in freshwater without adequate food (a greatly reduced feeding urge in freshwater and is a good evolutionary strategy for anadromous trout and salmon species because one of their greatest potential food supplies would be the young of their own species). Thus, one of the evolutionary adaptations that was acquired by early-run steelhead differentiating them from late-run fish that spawn soon after entering a river, is a life history that results in the accumulation of more energy reserves. Typically, they spend a longer period in the ocean. How does a steelhead "know" what race it belongs to. Why don't they spawn in any suitable stream indiscriminantly mixing and "homogenizing" all steelhead
in the basin into one common type? The strong homing instinct of salmonid fishes, made possible by a finely attuned sensory system, particularly the olfactory sense or sense of smell, returns the adult fish to the same tributary where they were born.

Without this well-developed homing instinct, steelhead could not segregate into discrete races and without discrete races, each specializing to utilize a specific part of a river basin, the steelhead could not make such effective use of the whole basin. Such an evolutionary strategy allows for greatly increased abundance and the depletion of evolutionary diversity by the elimination of certain runs causes an overall decline in abundance. Unfortunately, when a dam blocks several discrete runs, there is no practical way to maintain them all by hatchery propagation.
"Summer-run" steelhead occur in many rivers where they do not migrate far from the sea for spawning (perhaps 100 miles or less). The evolutionary selective pressure that would cause an ancestral common steelhead population to separate into heriditarily distinct summer-run and winter-run populations is directed by the species' "urge" to more fully utilize the whole river environment and thereby increase their abundance. For example, low flows in fall and winter may block access to the upper, headwater parts of a river system. Only those steelhead that migrate during the high flow period can spawn in the headwater areas. Thus, by having both spring or summer-runs and fall or winter-runs, steelhead trout can greatly increase their abundance in a river system because a considerably greater part of the drainage is utilized for spawning and rearing and each group specializes to best adapt to the specific environments of their particular sections.

In general, in rivers with both summer-run and winter-run steelhead,
the summer-run averages larger in size. The summer-run is the preferred race for angling because it is in freshwater for a longer period of time before spawning. Unfortunately, dams that block upstream runs and water projects that degrade flows and temperatures generally impact summer-run steelhead more than winter-run fish. Many rivers have lost their stocks of summer-run steelhead.

Cutthroat trout in lakes such as Flathead Lake, Montana, and rainbow trout in Lake McConaughy, Nebraska, may make spawning migrations of 100 miles or more. It is important that the homing instinct brings future generations precisely to the areas that insure best survival of eggs and young.

It is also a good evolutionary strategy for a species to have some flexibility in the expression of homing. In many small coastal streams inhabited by sea-run cutthroat trout, steelhead rainbow trout, and coho salmon, entrance into the "home" stream may be blocked by a delay in the fall and winter rains at the time the mature fish in the ocean are ready to ascend into freshwater. In such cases, wandering up and down the coast may occur until an "open" river is found. There appears to be considerable interchange (about $10 \%$ to $15 \%$ ) among the anadromous stocks of salmonid fishes between neighboring small coastal streams.

An unusual type of hereditarily determined movement can be found in young fish hatched in outlet streams of some lakes. Typically, trout living in lakes ascend inlet tributary streams where the young hatch and move downstream to the lake. If fish hatched in the outlet stream moved downstream they would not get back to the lake. In laboratory studies performed with eggs from inlet and outlet spawning stocks of the native cutthroat trout of Yellowstone Lake, and with similar stocks of sockeye
salmon from Karluk Lake, Alaska, it was found that the newly hatched fry derived from inlet spawning parents overwhelmingly oriented towards movement with the current (downstream movement) whereas the fry from outlet spawning stocks mainly moved against the current (upstream movement). These hereditarily distinct stocks of the same species in the same lake are possible because the homing instinct segregates the stocks at spawning and prevents interbreeding and "homoginization."

Many years ago I visited the Gorge Creek research station of the University of Alberta in the Canadian Rockies. The late Dr. R. B. Miller was conducting research to explain the relative rapid mortality suffered by catchable-size hatchery trout after stocking in a stream. He found that death was not from starvation, but from too much movement--the hatchery trout were "stressing" themselves to death. All suitable habitat areas in Gorge Creek were occupied by wild trout (protected sites with low velocity flow). The newly stocked hatchery trout milled about, continually seeking a habitat where they could rest. In the high gradient, fast flowing environment of Gorge Creek, few hatchery trout were successful in finding an adequate resting habitat and most died within a few days from exhaustion and high levels of lactic acid in their blood.

In rivers with slow-moving flow and large pools, hatchery trout would not be subjected to the same conditions as in Gorge Creek. The movements of large numbers of newly stocked hatchery trout milling about in a river, may be harmful to wild trout populations. The degree of harmful impact of stocked hatchery trout on wild trout is correlated with the density of the hatchery fish and the rate they are caught out by fishermen.

The two research studies I am familiar with on this subject concern the Madison River, Montana, and the Poudre River, Colorado. The Madison River study by Dick Vincent of the Montana Fish and Game Department presented strong evidence that the stocking of catchable rainbow trout resulted in reducing the numbers of wild brown and rainbow trouts. The Poudre River study was made by Larry Marshall as part of his graduate research program at Colorado State University. Mr. Marshall compared the wild brown and rainbow populations in stocked and unstocked sections of the Poudre River and found no differences. The two studies are not really contradictory. The resolution of the apparent contradiction lies in the differences in the intensity of stocking and the rate of catch of the hatchery fish in the two rivers. The Madison River stocking was made once or twice a year. The stocked sections received a massive number of catchable rainbows, about equal to the total biomass of wild trout in that section. Fishermen caught only about $15 \%$ of the stocked fish. In the stocked sections of the Poudre River, on the other hand, stocking occurred every two weeks. Each stocking equalled about $10 \%$ of the wild trout biomass. About $90 \%$ of the stocked fish were caught before the next plant.

In the Madison River, an unnaturally high density of trout was maintained for a prolonged time. Under such circumstances the resident wild trout would be expected to respond by continually driving the hatchery fish away from their territory or microhabitat. After numerous encounters it can be assumed that many wild fish became severely stressed and abandoned their territories. Such fish would be highly vulnerable to predation and disease.

An ironic part of the Madison River study was the finding that less
than $1 \%$ of the hatchery trout survived to the following year. The combined numbers of hatchery and wild trout in the stocked sections (before the next stocking occurred) was much less than the numbers of wild trout alone in the unstocked sections.

## Sensory Systems

Fish have about the same sensory organs to receive and interpret external stimuli as do terrestrial vertebrates such as man, but the structure of the sensory organs may differ considerably because the fish's organs are designed to function in water. Fish also have a special sensory system, the lateral line, that is not found in terrestrial animals.

Because of the density of water in comparison to air, sound waves travel five times faster and further in water than in air. An object moving through water creates a disturbance or displacement effect exceedingly greater than would be created by the same size object moving through air. The lateral line organ consists of sensory hairs that detect the pressure waves from movement. It serves as a remote sense of touch. The lateral line is not used as a "hearing aid" as is commonly believed. Sound waves, unless the origin is very near, are too feeble to be detected by the lateral line sensory hairs. The lateral line system of trout is well developed, but the highest development of the lateral line system is found in blind cavefishes and deep-sea fishes where vision plays little or no role in finding food. The movements from a single water flea of 1 mm in size can be detected, the organism located and consumed by a blind cavefish in an aquarium.

Vision is the main sense used by trout in feeding, but may be supplemented
and sometimes replaced by the lateral line and the sense of sme 11 for feeding. I have observed rainbow trout in lakes that had such heavy development of cataracts in the cornea of the eye from parasite infestation that their vision must have been so impaired to be virtually useless. Yet these trout were in good condition and well-fed. They had consumed mainly the relatively large crustacean Gammarus. The lateral line system of trout is sufficiently sensitive to easily detect movement by Gammarus and to locate the prey for consumption. These "blind" trout were readily caught by anglers using bait such as cheese and salmon eggs. I assumed that the sense of smell lured the "blind" trout to the bait.

The vision of trout is acute; a fact that all anglers are well aware of. The retina of the eye, similar to our own retina, has both rod cells for vision in dim light and cone cells for color vision and discrimination of finer details in bright light. The anatomical structure of the eye of trout is particularly well adapted to detect movement and it seems to have the ability to simultaneously focus on two objects at near and far distances.

Although most species of trout feed both during the day and after dark, the eye of rainbow trout and cutthroat trout is more specialized for day feeding and the eye of brown trout more specialized for feeding in dim light and darkness. The structure and visual pigment in the retina of the eye of brown trout gives it optimum sensitivity in dimmer light.

Salmonid fishes have an amazing olfactory sense or sense of smell. This extreme sensitivity was discovered when homing in salmon was being studied. It was found that when ascending rivers on their spawning migration, the correct choice in the selection of one tributary stream rather than another, was made by olfaction. The difference in "smells" between two
neighboring tributaries appears so insignificant to our own sense of smell that it seems incredible that trout and salmon can indeed smell the difference. Further research demonstrated that trout and salmon can detect odors diluted to concentration of 1 molecule of odor in trillions of molecules of water. Such sensitivity is many fold greater than found in man.

Other, little understood senses also play a role in homing and orientation. It is still not completely known how a steelhead trout or salmon 1000 miles or more from the coast can migrate back to the mouth of its "home" river (where the sense of smell can take over and lead the spawners to their home tributary). Their detection of and ability to orient to polarized light may play a role, but it also seems likely that trout and salmon can detect and orient to gravitational fields by some unknown sensory mechanism.

Yellowstone Lake cutthroat trout spawners were removed from their "home" tributary, blinded and their nostrils plugged (the senses of vision and olfaction could not be used) and then released in the lake some distance from their home tributary. Most of the experimental trout found their way back to their home tributary--they did not move randomly to spawn. It was speculated that trout without the senses of sight or smell could find their home stream by hearing (or perhaps "feeling" with the lateral line) the sounds and turbulence differences made by different tributaries entering the lake.

The auditory sense or sense of hearing is not as important to a trout as its sense of sight, smell, and lateral line. The hearing range of trout and most fishes tested is comparable to older humans that have lost their hearing sensitivity to higher frequency sounds. The inner ear of fishes
is similar in structure to our own inner ear with three "semicircular canals" and associated sac-like structures that function as both an organ of balance (gravity detection) and an organ of hearing. Otoliths are small "bony" structures of balance found in the sacs at the base of each semicircular canal. Otoliths are generally the best part of the trout's anatomy to use for accurate ageing.

Because sound waves travel much more efficiently in water than on land, and sound waves penetrate a fishes' body with little disruption because the fishes' body consists mainly of water (that is, the sound waves are not disrupted by passing from one medium to another of different density), there is no need for an outer ear and a middle ear in fishes to assist in capturing and transferring sound waves into the inner ear. Some indication of sounds a fish might hear can be had from sitting underwater and listening. The greatly increased effectiveness of water as a medium to transport sound waves in comparison to air can be readily perceived by sitting underwater and tapping two rocks together. Sounds from above the surface such as persons talking can be detected, if at all, only as muffed noise. Sounds of terrestrial origin are refracted from the water's surface due to the different densities of air and water.

The sense of hearing probably plays a role in the behavior of trout such as territorial defense. Sounds have been recorded from salmon on spawning redds. The sounds are probably derived mainly from muscles striating over the air bladder (similar to rubbing fingers over a baloon), and function as a means of communications.

The main function of the air bladder in trout is that of a hydrostatic organ. It gives neutral bouyancy and balance. That is, when properly
adjusted, the trout's body is weightless, and it remains in a constant, upright position without any energy expenditure to resist sinking or rising to the surface. The internal pressure of the air bladder must be maintained about equal to the external pressure. Because of the density of water, the atmospheric pressure at the surface ( 14.7 pounds per square inch $=1$ atmosphere) increases by one atmosphere for every 33 feet of depth. Thus, a fish descending to a depth of 100 feet in a lake has a pressure in its air bladder three times greater than the pressure at the surface. Gas pressure is adjusted by a network of capillaries that excrete gas into or reabsorb gas from the air bladder. This adjustment is not instantaneous. A fish caught at 100 feet and hauled rapidly to the surface would suffer from a greatly expanded air bladder. The external pressure at the surface is only one third the pressure at 100 feet, thus the volume of the air bladder would increase three fold by such an instantaneous change. Of all salmonid fishes, the lake trout probably has the most specialized air bladder for living at great depths. In Lake Tahoe and Great Bear Lake, Canada, lake trout have been netted at depths of more than 1300 feet where the external pressure is 40 times greater than at the surface.

One of America's first "scientific" anglers, Edward R. Hewitt, believed that the influence of barometric pressure on trout's feeding could be explained by changes in the air bladder volume. He reasoned that on low pressure days, the air bladder of a trout would increase in volume and squeeze against the stomach leading to a reduction or cessation of feeding. Although changes in atmospheric pressure are transmitted below the surface of the water, the greatest change possible in atmospheric pressure is only
equal to the pressure change resulting from ascending or descending three feet in water. Thus, a trout rising or descending three feet is subjected to the maximum pressure change possible if atmospheric pressure could instantaneously fluctuate by the greatest known extremes. There is no doubt that a fish's air bladder is extremely sensitive and atmospheric changes can be detected, but any influence of atmospheric pressure on feeding is more likely by an indirect influence, such as effects on movements of invertebrate animals.

As has been mentioned, the brain of trout, as in all fishes, is primitive in structure. There appears to be no area of "gray matter" where any form of conscious thought process might occur. It is designed to receive, assimilate, and act on external stimuli without asking "why" and "how." This raises fascinating questions on the relative intelligence of different species of trout and on the possibilities that fishing acts as a selective factor weeding out the "dumb" individuals generation after generation until the race has a hereditary basis for being "smarter"--or at least more difficult to catch.

The results of numerous studies leave no doubt that different species of trout have different degrees of susceptibility to being caught by fishermen. When more than one species occurs in the same waters, brown trout are caught in the least proportion to their numbers in comparison to other species. In general, rainbow trout are more difficult to catch than brook trout, and brook trout are more resistant to catch than cutthroat trout. It has long been reasoned and generally accepted as fact that man's fishing for brown trout in Europe for many hundreds of years has acted as a force for selective breeding of "smarter" fish.

Although fishing as a selective factor is indeed possible and even probable according to the laws of genetics, I find serious flaws in such a simple explanation. If the degree of vulnerability to anglers' lures and baits is directly related to the length of time a species (or race of a species) has been exposed to angling, then eastern brook trout should be more difficult to catch than rainbow trout. The brook trout has been exposed to fishing by man about three times longer than has the rainbow trout. Widespread angling for rainbow and cutthroat trouts has come about only during the past 100 years.

Quantitative data is lacking to adequately settle the issue. I have little doubt that at least under controlled, laboratory conditions, a race of any species of trout can be selectively bred to be more difficult to catch on lures. However, in nature, trout must be opportunistic and take split second action if they are to get their share of food. To be too cautious in the selection of food items could lead to starvation and the loss of "too cautious" hereditary material to the next generation. Selection works both ways.

It is likely that most of the differences in susceptibility to being caught by anglers is a reflection of innate behavioral patterns rather than "intelligence." For example, the preference of brown trout for cover, deeper waters, and nocturnal feeding, especially when living with rainbow or cutthroat trout, makes the brown more difficult to catch, except by those anglers who have specialized in learning the details of the feeding habits of brown trout in a particular section of a river.

## Evolution and Heredity

Several references have been made to evolution in relation to changes and specializations in hereditary traits such as feeding, reproduction, and migration. Evolution is the result of hereditary changes brought about by natural selection to better adapt a species (or any segment of the species) to its environment. A popular misconception of evolution concerns the term "survival of the fittest." "Fit" is commonly assumed to imply big, strong, and fierce--the survival of the biggest, the strongest, the fiercest. A bit of reflection on this concept readily reveals some faulty logic. The biggest and fiercest of the dinosaurs became extinct with all other dinosaurs while some of the groups of small, inconspicuous surviving reptiles gave rise to birds and mammals, the dominant vertebrate life on earth. In the oceans, sharks are the largest and fiercest fishes but many millions of years ago, sharks were larger and more abundant. Presently, sharks represent only a small fraction (perhaps 2 or $3 \%$ ) of the biomass of all fishes in the oceans. The bulk of fish biomass is made up of small fishes such as herrings, anchovies, and sardines that feed at low trophic levels and reproduce rapidly and abundantly. There is much evolutionary truth to the biblical saying that the meek shall inherit the earth (and its waters). In evolution, "fittest" means leaving the most offspring (those most successful in passing on sets of unique hereditary material to the next generation). Different species evolved different strategies to insure successful reproduction, but large size and fierceness, by and large, has not been a highly successful strategy. It is not good evolutionary strategy to expend excessive energy on fighting when it could be better used in feeding and reproducing. There is also much evolutionary truth in the popular phrase: "make love not war."

The list of endangered species in the United States is full of the largest and fiercest species of their kind such as grizzly bear, wolf, eagle, falcon, and Colorado River squawfish--the largest and most predatory species of the minnow family in North America and now largely replaced by small species of introduced minnows that are more successful at leaving offspring than is the squawfish.

This discussion on evolutionary strategy leads to an area of biology that has long fascinated me and an area that holds much significance for modern fisheries management. What are the mechanisms that allow two or more species to live together in some environments while one species may replace other species in other environments? For example, brown trout and rainbow trout have replaced the native brook trout in a large part of their native range in the East and brown, rainbow, and brook trouts have replaced the native cutthroat trout from almost their entire native range in the Rocky Mountain region. Under the misinterpretation of "survival of the fittest," many anglers and writers perceive the replacement of brook trout by brown and rainbow trouts as the result of larger, more aggressive browns and rainbows driving out the smaller brook trout in one one combat. This is simply not the case. In small, cold streams the environment favors the evolutionary heritage and reproductive strategy of brook trout and they leave more offspring and are dominant over brown and rainbow trouts. In larger, warmer rivers the environment favors the brown and rainbow trouts over the brook trout and "fighting" has nothing to do with which species "wins."

The environment determines which species of trout will be favored and it determines the relative success of "trout" (all species) in
competition with other fishes. A study made on Otter Creek, Nebraska, a tributary to Lake McConaughy, nicely illustrates this point. In 1969 Otter Creek suffered from the impact of overgrazing by cattle. The banks were eroded and denuded of vegetation; the stream was silted, turbid, and ran shallow, wide and warm. The 1969 fishery survey revealed that $98 \%$ of the fish biomass in Otter Creek consisted of various species of minnows and suckers and $2 \%$ consisted of trout. The environmental conditions gave a definite advantage to minnows and suckers over trout. In 1969 the state fishery agency leased land along the creek and constructed fences to keep livestock away from the stream. Riparian vegetation rapidly came back, shading and cooling the water; the root system forced the stream channel to deepen and narrow. Erosion was greatly reduced and the stream ran clear, exposing clean gravel. By 1974, Otter Creek naturally produced 20,000 yearling rainbow trout smolts which migrated to Lake McConaughy. About $98 \%$ of the fish biomass in Otter Creek now consisted of trout and about $2 \%$ of minnows and suckers. It is clear from the Otter Creek example that no other strategy could really work to favor trout over the other species; no amount of eyed egg planting, poisoning of non-trout species, or catch-and-release regulations could have permanently tipped the advantage to favor trout. Only a change in environmental conditions that favor trout in competition for food and space with other species can be truly successful in reversing species dominance in such situations. The evolutionary heritage of salmonid fishes makes them well-adapted to cold, clear water environments. If we are to maintain and improve our trout fisheries, the major emphasis must be given to maintaining or creating the environments that favor the evolutionary adaptations of trout over other species.

In the previous section I discussed the possibility that fishing might act as an evolutionary selective factor to "weed out" the most readily caught individuals in a population. Another frequently expressed concern is that many fisheries may be selecting against the largest, fastest growing individuals thus favoring the "runts" in the population. The argument typically is expressed along the following lines: A farmer that continually kills his biggest and best animals and only allows the runts and misfits to breed future generations would soon be out of business. At face value such an analogy seems a valid assessment of the potentially harmful consequences of a fishery acting as a selective factor against the "biggest and the best" in the population. The logic, however, is faulty. There is little valid analogy between domesticated strains of plants and animals selected and "genetically improved" for controlled environments and wild species surviving in nature. For example, what would be the results if the "biggest and best," the most "improved" strains of corn or wheat or sheep and cattle were planted in wild, natural environments to compete with wild species and be exposed to predation on a year-round basis without cultivation, irrigation, pesticides, herbicides, supplementary feeding and protection? Survival would be nil (this is essentially true also for highly domesticated hatchery trout stocked into natural environments). What we frequently view as "genetic improvement" is actually genetic degradation in the evolutionary sense where survival is the name of the game.

There is no doubt that growth rate and size has some hereditary basis. By selection it is possible to create smaller or larger races such as ponies from horses, bantam chickens from normal chickens, and within the single species of domestic dog, a wide range in sizes can be observed
in the various breeds. There is even a race of dwarf humans, the pygmies of Africa. The genetics of growth and dwarfism is well known. Typically only a very few hereditary units or genes determine growth and thus hereditary modification in size can be rapid. Strains of fast growing and slow growing hatchery trout can be produced in only one or two generations of hatchery selection.

Despite all of the theoretical and actual evidence that it is possible, if not probable, that fishing mortality acts as a selective factor favoring hereditary change in a trout population for slower growth and smaller size, I know of no data demonstrating that such a phenomenon has even occurred in a wild trout population. I believe this is due to the fact that wild populations are under natural selection and natural selection would strongly select against hereditary change (unless environmental conditions change). Thus, angler induced selection favoring hereditary factors for growth much below the population norm would have to be extremely intense. For example, all trout of normal or above normal growth would have to be removed from the population before they spawned. No fishery that I know of can produce that kind of selective intensity.

A trout population that was long exposed to an excessively high angler kill is the native cutthroat trout resident in the Yellowstone River just downstream from Yellowstone Lake (and to a somewhat lesser extent the cutthroat populations living in Yellowstone Lake proper). If the effects of fishery induced hereditary growth changes were to be evident on any wild trout population it should be evident in the Yellowstone River cutthroat trout. In 1974 catch-and-release (no-kill) regulations were instituted on the Yellowstone River cutthorat population. These regulations greatly
reduced the level of angler-induced mortality and within a few years the growth and maximum size of the largest fish (about 22 inches and 5 pounds at six or seven years of age) was similar to what was reported when this population was first fished 100 years earlier.

Another line of evidence concerns the numerous examples of severely stunted trout transplanted into a formerly barren pond or lake with good environmental condions and an abundant food supply where they undergo an amazing spurt of growth, often two or three pounds in a year. The trout may have been stunted but they were not hereditarily "runted." Such a rapid increase in growth of stunted trout when placed in a new environment with abundant food is impressive to observe. Several years ago I had a small pond constructed on my property. While the new pond was still filling, I stocked it with about 20 stunted brook trout. These were sexually mature fish of about 5 to 7 inches taken from a small stream being poisoned prior to stocking with native cuthroat trout. Within four months these trout grew to 10 and 12 inches and completely changed their shape from a slim body to a deep bodied form. It was difficult to believe they were the same fish that had grown only 5 to 7 inches in three or four years. They about quadrupled their weight in four months in a new environment.

The most frequently cited example of a fishery causing hereditary changes, reduced growth, and smaller maximum size in a wild trout population concerns the brook trout in the Au Sable River, Michigan. A paper was published in a scientific journal presenting mathematical formulas which added considerable credibility to the belief of many anglers that the present day brook trout in the Au Sable River do not grow as large as they did in the good old days. It has been commonly assumed that the present
small size is the result of overfishing and selective removal of the "biggest and best" of the breeding stock for many generations. I would not argue that theoretically such a phenomenon is possible (the condition of the mathematical model mentioned above, however, is that only very few hereditary factors or genes determines growth--whereas the actual genetic determinants in a wild population are much more complex). I doubt, however, that the Au Sable brook trout have been genetically changed by angling pressure so that they now have a hereditary basis for slower growth than the population had 60 or 80 years ago. The fishery statistics I have seen on the Au Sable River fishery do not indicate an excessive kill of brook trout by anglers. Mortality from predation by large brown trout and predatory birds and mammals is higher than fishing mortality. If these small Au Sable brook trout were to be transplanted into a new, food-rich environment, I am confident that it would be demonstrated that they have not lost the inherited potential for more rapid growth.

I do not doubt that there is a real basis for the anglers' belief that a hereditary change has occurred in the Au Sable brook trout. They do not grow as rapidly or attain such a large size as they did many years ago. Logical explanations can be made, however, to interpret what has happened.

Brook trout were not native to the Au Sable River (grayling were native and they became extinct soon after the brook trout were introduced). Brook trout were stocked before the turn of the century. As is often typical of a newly introduced species in a new environment that provides all the necessary requirements the brook trout flourished, its population greatly expanded, growth was good, the fishery was excellent. Around the
turn of the century, brown trout were introduced into the Au Sable. There is considerable overlap between the brown trout niche and the brook trout niche. As the brown trout population expanded it did so largely at the expense of the brook trout population. Brown trout claimed an increasing share of the food supply and the better habitat sites. With environmental changes in the watershed, water quality was degraded and these changes favored the brown trout over the brook trout. I know of no way to test or prove alternate theories to everyone's satisfaction, but from a review of the evidence, I believe the lessened quality of the present Au Sable brook trout fishery is most simply explained as a result of environmental changes, particularly those that favor brown trout over brook trout and not from a hereditary change induced by angling.

The environmental factors that act as selective agents to effect subtle hereditary changes in a trout population making it more perfectly adapted to its environment are often difficult to interpret. In most cases only intelligent speculation can be made. In recent years I had the opportunity to examine how the influence of "coevolution" or the evolutionary interaction between species, long existing in the same environment, might act to better adapt the species to specific environments and thus making them more resistant to replacement by introduced species.

I was involved in a research project in Glacier National Park to determine what waters still had populations of the native trout and the extent of their replacement and hybridization by non-native trouts. Beginning about 1920, a massive fish stocking program was initiated in Glacier Park. Many species of salmonid fishes were stocked but the eggs and fry of Yellowstone Lake cutthroat trout were stocked in the greatest
numbers. At the time it was not realized that the cutthroat trout of Yellowstone Lake represented a different subspecies. That is, it did not belong to the same geographical race as the cutthroat trout native to Glacier Park.

In lakes that were originally barren of fishes, the Yellowstone cutthroat became established and still flourish. In lakes that had populations of the native cutthroat trout I could find no trace of Yellowstone cutthroat or evidence of hybridization despite the stocking of millions of Yellowstone Lake trout in these lakes over a 20 to 30 year period. Obviously, the environments of these lakes must greatly favor the native cutthroat trout over the introduced Yellowstone trout. I noted that the intestinal parasites in the native trout were very different from the parasites native to Yellowstone Lake. It can be assumed that the native trout and its parasites have evolved together for thousands of years in the Glacier Park lakes. In such a situation it is likely that the harmful effects of parasite infestation would be less on the native fish that has lived with and adapted to these parasites than on introduced fish never before exposed to these species of parasites in their evolutionary history.

I also noted that the lakes with native cutthroat trout also had populations of the bull trout, a large, predatory salmonid related to the Dolly Varden. In one lake I observed bull trout attempting to prey on the native cutthroat trout. Large numbers of 5 to 8 inch cutthroat trout occurred along the shoreline of the lake. When large bull trout approached them the small cutthroat would form a dense school in open, deep water. The bull trout would try to herd the school into shallow water but when they approached too close, the school would "burst" apart with the individuals
forming another compact school out in deep water again. I never observed the bull trout actually attacking unless the cutthroat were in shallow water. I assume that this unusual schooling behavior I observed in the cutthroat trout native to Glacier Park lakes is a hereditary defensive mechanism against bull trout predation. Trout, such as the Yellowstone Lake cutthroat trout that evolved for thousands of years in Yellowstone Lake with no other fishes, would lack a defense specific to bull trout predation and when introduced into a lake with bull trout they would be selectively preyed upon.

Races of trout that have a long evolutionary history in large lakes or as anadromous stocks in the ocean would be expected to evolve special adaptations to be effective predators and reach a large size. In all the common species of trout the propensity to attain a large size can be noted among certain races. The largest rainbow trout are certain races of steelhead (those that have the life hstory characteristic to forage for two or more years in the ocean before first spawning) and the "Kamloops" trout native to large lakes of British Columbia. The largest of all cutthroat trout is the race native to the Lahontan basin which specialized as a top predator in ancient Lake Lahontan for about 50,000 years or more. Among the brown trout, the populatons native to the Alpine lakes of Europe (with abundant populations of whitefishes for forage) and the brown trout native to the Caspian Sea basin have produced specimens much larger than the official rod-caught record. In the Caspian Sea, the brown trout is represented by sea-run populations that have life history characteristics similar to our Pacific Coast steelhead. Different "runs" of the Caspian trout have different life history characteristics and attain different
average and maximum sizes. Evidently the "winter-run" that once migrated up the Kura River attained the largest size. The Russian literature claims a maximum size of more than 100 pounds for Caspian trout but such a size is not authenticated and is probably an exaggeration. The fishery statistics of the commercial catch, however, leaves no doubt that Caspian brown trout are large. The average size of specimens caught from the winter-run in the Kura River in 1916 was 33 pounds.

The abundant forage fishes in the Caspian Sea are species of the herring family, similar to North American shad and alewives. Could a Caspian brown trout stocked into Lake Michigan with its great abundance of alewives reach a weight of 50 pounds or more? The giant Caspian brown trout is now very rare. Dams, water developments, and pollution have exterminated most of the runs. There is no indication that the cause of natural resource conservation fares better under a socialist government.

Among the brook trout, the races associated with large lakes of the Great Lakes region and Hudson Bay typically have longer life spans and reach a much greater size than do the more southerly populations of brook trout. That these differences are hereditary and are of fisheries management significance has been clearly demonstrated by the work of Dwight Webster and Bill Flick of Cornell University. Several years ago Webster obtained eggs from brook trout native to two large lakes in the Hudson Bay drainage. These wild, Canadian brook trout were stocked into several private ponds and lakes in the Adirondacks and their performance compared with hatchery brook trout. The Canadian trout lived about twice as long, reached about twice the size, and yielded three to six times more biomass from similar stockings than hatchery brook trout. Webster and Flick have
been conducting these studies for many years. They have presented their data at fishery meetings and symposia; they write annual reports detailing the results and have published papers in scientific journals. The demonstrated superiority of the wild Canadian strains of brook trout in the Adirondack lakes is beyond dispute, yet we are still waiting for a state or federal trout propagation program to utilize these basic concepts in a major way to improve the hatchery product and increase the survival and growth of stocked trout.

Many anglers, at least vaguely aware of some of the points discussed above, have demanded a better hatchery trout. The problem is, however, that there is considerable confusion concerning just how to go about creating a "better" hatchery trout. The most pertinent question concerns the intended use of the hatchery trout. For stocking catchable-size fish for instant return where growth and long term survival is of no consequence, the cheaper the better. Most present domesticated strains of hatchery trout are well adapted to low cost production. Not much "improvement" can likely be made. It would be foolish to try to propagate a race of wild trout for the production of catchable trout. Costs would probably double.

The stocking of fingerling fish in lakes and impoundments to survive and grow for one to several years is another matter and the genetics or hereditary background of the fingerlings play a major role in determining their growth and survival. For benign environments with an abundance of food, no competing fish species, and few or no predators (more-or-less an extension of a hatchery raceway), the domesticated hatchery trout would likely grow better (at least for the first year) than wild strains. They have been selectively bred to be gluttons. In such situations I foresee
the domesticated trout will continue to be the "best" trout to stock. Even in such "benign" environments, however, the fishery would likely be improved if certain wild strain fingerlings were stocked with the domestic trout because they would have a greater maximum age and attain a greater maximum size.

In those waters with abundant populations of competitor and predator species and with marginal trout environments, where survival of domesticated fingerlings is extremely low, the creative use of certain wild trout strains with hereditary adaptations to cope with these conditions should become a major fisheries management technique. Some agitation and pressure from anglers and angling organizations will help speed this process.

Many have the fantasy that it is possible to create a "supertrout" or a "trout for all seasons" by selective breeding in a hatchery. There never can be such an animal. What may be "super" in one environment may be a complete failure in another. The most widely known hatchery "supertrout" is the stock of rainbow trout selectively bred for many generations at the University of Washington's hatcher--commonly known as the Donaldson rainbow. This trout is superbly adapted to the University of Washington's hatchery environment and its artificial diet. It may grow to 10 pounds or more in two years in the hatchery. Many angler clubs, state fishery agencies, and foreign governments clamored to get eggs of the Donaldson rainbow so they could populate their lakes and streams with giant rainbow trout. From previous discussions it should be understandable why the Donaldson rainbow has the survival instincts of a dodo bird when stocked into natural waters with competitors and predators. A series of studies in California clearly demonstrated that survival in
the wild is negatively correlated with the degree of domestication of hatchery strains of rainbow trout. That is, the longer a strain has been under hatchery selection, the less is the survival of its offspring in the wild. A comparison was once made in two farm ponds in Utah, stocked with fingerlings of Donaldson rainbow and fingerlings of an "ordinary" strain of hatchery rainbow (from the Jones Hole, Utah, National Hatchery). The fish were marked for correct identification and sampled every six months for two years. No artificial feed was given. At each sampling period the "ordinary" strain averaged $25 \%$ larger in one pond and $50 \%$ larger in the other. If this comparison had been conducted at the University of Washington's hatchery and with their diet, I am confident the results would have been reversed. There is obviously much more influence on "growth" in trout in natural environments than that governed by a single unit of heredity.

Once a brood stock of trout is raised in a hatchery, selection or a change in their heredity is, essentially, unavoidable. Selection occurs for the acceptance and utilization of an artificial diet and for disease resistance. Even when eggs are taken from wild races and the young reared only for a year or two in a hatchery before release--such as in the propagation of steelhead trout and coho salmon--harmful selection may occur. How such selection occurs is illustrated by a study of coho salmon in Oregon. It was found from examination of transferrin, a compound in the blood, that three types of transferrin were present in Oregon coho salmon that can be designated as types $A, B$, and $C$. It was found that almost all wild coho returning from the ocean had types $A$ and $B$ whereas the young coho raised in the hatchery had a high proportion of type C. It was then
discovered that type C transferrin gave resistance to a bacterial iniection. The presence of the bacteria in the hatchery water and the high density of the young coho promoted an outbreak of the disease which resulted in an intense selection for those individuals with the $C$ type of transferrin-the type that, for some unknown reason, has a low survival value in the ocean. A recent publication on a hatchery brood stock of native cutthroat trout in Montana revealed that half of the genetic or hereditary diversity that could be measured from a study of protein molecules, had been lost in about 15 years of hatchery propagation since eggs were taken from a wild stock.

The point is that if we are to make use of the hereditary diversity and specializations of wild races of trout in a propagation program, brood stocks should be maintained in natural waters under natural selection or the desirable attributes we seek may be lost by hatchery selection.

First, however, we need to have greater emphasis given to wild trout management in state fishery programs. Pat Coffin, biologist with the Nevada Fish and Game Department accompanied me when I caught the native redband trout in Chino Creek in water of $83^{\circ}$. Pat wrote an article on these trout in a 1975 issue of Nevada Outdoors magazine. He concluded that such a trout... "may have eventual fisheries management implications when fisheries management becomes sophisticated enough to appreciate this unique trout." I wouldn't advise waiting until the level of sophistication is properly elevated in the field of fisheries management before we appreciate and utilize wild races of trout--I would be satisfied with people who are willing to try something new, work hard at it, and have a good measure of common sense.

## CLASSIFICATION

I approach the writing of this section with some hesitation and trepidation. The science of classification or taxonomy is a subject little understood even by most professional biologists. Basically, taxonomy establishes a system for the precise identification or placement of an organism within a larger scheme (The Animal Kingdom). It works somewhat similar to a mailing address (or zip code) that allows for the correct placement of any address in the world by levels of "inclusiveness." For example, the country, state or province, city, town or village, street, and number on the street.

The Animal Kingdom is divided into phyla (singular phylum) which segregates the earliest branches of the evolutionary tree such as protozoa, jellyfish, worms, molluscs, arthropods (insects, spiders, and crustaceans), and starfishes. Vertebrate animals belong to the phylum Chordata which consists almost entirely of vertebrates except for a few small marine organisms such as sea squirts. Vertebrates are divided into classes. There are three classes of living fishes: one class for about 50 species of jawless fishes (lampreys and hagfishes), one class for about 600 species of sharks, rays, and chimaeras (the cartilaginous fishes), and one class for about 25,000 species of bony fishes. A class is further divided into orders and an order into families. Trout are part of the family Salmonidae which, along with many other families of fishes such as pike, smelt, and a diverse array of bizarre deep-sea fishes form the order Salmoniformes. I wrote the section on the order Salmoniformes for the most recent edition of the Encyclopaedia Britannica and must admit that there is considerable confusion and uncertainty concerning the most correct classification of
fish families currently grouped under the Salmoniformes.
I subdivide the family Salmonidae into three subfamilies: one for whitefishes, one for grayling, and one for salmon, trout, and charr. The major evolutionary lines within the subfamily Salmoninae are recognized as genera (singular genus). For those anglers who yearn to fish for rare or little known trout-like fishes in exotic places I would suggest the genera Hucho, Brachymystax, and Salmothymus. Three or four species of the genus Hucho are known. One occurs in the Danube River basin of Europe, one (known only from one specimen) evidently is native to the headwaters of the Yangtze River, China, and another species is found in northern Japan northwards to the Amur River. The Siberian "Huchen" or "taimen" inhabits all of the large rivers of Siberia. I classify the Siberian huchen in the same species with the Danube huchen (two subspecies of one species). The Siberian huchen has been known to attain weights of up to at least 120 pounds. The European-Siberian huchen and the king salmon are the species that attain the greatest size and weight in the family Salmonidae.

The genus Brachymystax occurs across Siberia eastward to the Amur River and northern Korea. The Russian common name for fishes in this genus is "lenok." The lenok feed mainly on invertebrates and reach a maximum weight of about 8 pounds. Trouts of the genus Salmothymus are relatively small fish (up to about 3 to 4 pounds). They somewhat resemble a cross between a trout and a grayling (thus the basis for the name of the genus) and have a limited range in tributaries to the Adriatic Sea in Yugoslavia.

Three genera of salmonid fishes are native to North America: Salmo
(Atlantic salmon, brown, rainbow and cutthroat trouts), Salvelinus (brook trout, lake trout, Dolly Varden, and Arctic charr), and Oncorhynchus (Pacific salmons).

A "good" classification should be an accurate reflection of degrees of relationship so that an evolutionary diagram can be made to illustrate all of the branchings from a common ancestor leading to all the living species within a group such as a family, subfamily, or genus. To accomplish this I separate the trout species in the genus Salmo into subgenera. The subgenus Salmo includes the brown trout and the Atlantic salmon, and the subgenus Parasalmo includes the cutthroat and rainbow trouts. I also recognize a subgenus Platysalmo (the "flathead" trout) that I named for one species known only from one river in Turkey.

It can now be envisioned how the native trouts of western North America are collectively classified as a subgenus--Parasalmo within the increasingly more inclusive levels of genus, family, order, etc.. So far, so good. The real problem comes when trying to organize Parasalmo into its constituent species and subspecies. As was previously mentioned, there is no definition of a species that can be strictly used to authoritatively decide which groups of trout should be recognized as species. The most commonly used definition of an animal species is that of a group or groups of animals that interbreed with each other (or at least would interbreed if geographically isolated populations occurred together) but not with other species. The main test for species recognition then is the ability to live together with its most closely related "species" without hybridizing. The strong homing instinct of salmonid fishes allows various groups with only very slight hereditary differences to live together
without hybridizing. For example, summer-run and winter-run steelhead rainbow trout may utilize the same river with resident, non-migratory rainbow trout with all three groups maintaining reproductive isolation from each other. Should they be classified as three different species? The problem here is that all members of a species should be derived from a single common ancestor. If all winter-run steelhead were derived from a common ancestor, if all summer-run steelhead came from another common ancestor, and all resident rainbow trout originated from a third common ancestor, then they should be recognized as three, separate species. It is obvious, however, from an evaluation of all the evidence of relationships that this is not the case. In most river systems, all of the three ecological forms of rainbow trout are more closely related to each other than they are to similar ecological forms in other rivers. That is, over thousands of years, a common ancestor rainbow trout gave rise to diverse ecological forms in each river system and, given sufficient time to evolve hereditary differences, one form can give rise to another. In such situations it is most correct to classify all of the closely related forms as members of one species.

Although there is no "law" against it, the three ecological forms of rainbow trout should not even be classified as different subspecies. Subspecies are geographical races of a species that have been isolated from other races of the species long enough to evolve recognizeable differences. but not long enough to differentiate to a degree that they would avoid hybridization with their nearest relatives if they came into contact. Glearly, the ecological forms of rainbow trout found in Pacific Coast rivers are not geographically isolated races--all forms occur together
throughout most of the range of the species.
The significant conclusion to be drawn from this is that there is an enormous amount of hereditarily based diversity among native trout populations governing ecological and life history traits such as migration, time of migration, tolerances of temperature extremes, predatory specializations, etc., and this diversity is not formally recognized with scientific names associated with species and subspecies. Taxonomy is a relatively simple system for grouping and classifying according to degrees of relationship. According to the rules of taxonomic nomenclature, the subspecies is the lowest level of classification. Our taxonomic system is simply not designed to adequately categorize all of the finer levels of evolutionary diversity found within a wide-ranging species such as the rainbow trout. However, it is apparent to anglers who fish extensively for the different ecological forms of native rainbow trout in Pacific coastal states that, as a practical matter, these races can be considered as if they were entirely different species because of the differences in life history. The same is true for fisheries management agencies. Each specialized form--the different runs of steelhead, resident river trout, and lake specialized populations--should be managed as if each were a different species.

The American Fisheries Society's check list of North American fish species recognizes six species of trout native to western North America-rainbow trout, Salmo gairdneri, cuthroat trout, S. clarki, California golden trout, ́. aguabonita, Gila trout, ㅇ. gilae, Apache or Arizona trout, S. apache, and Mexican golden trout, $\underline{\text { S }}$. chrysogaster. This classification is, at best, only a rough approximation of actual degrees of relationships
and evolutionary reality. The only two "species" that can live together without massive hybridization are the rainbow trout and the cutthroat trout--but even here, only one of the 15 subspecies of cutthroat trout (the coastal cutthroat trout) occurs with rainbow trout over a wide geographical area. In interior waters, introduced rainbow trout have hybridized with the interior subspecies of cutthroat trout until the native cutthroats are now very rare and some are probably extinct.

There have been trends in the classification of western trouts ranging from including all of the diversity as a single species (or more commonly two species--rainbow and cutthroat) to the recognition of more than 30 separate species. These fluctuating trends of trout classification during the past 100 years is reflected in the considerable confusion and errors frequently found in both the biological and angling literature in matters relating to trout taxonomy.

America's most eminent ichthyologist or fisheries scientist, David Starr Jordan, who was also the first president of Stanford University, exerted the dominant influence with his schemes of trout classification from about 1880 to 1930. With the great variability found in our western trouts, it can be readily understood that early attempts to classify all of this variability into species and subspecies would be fraught with confusion. Jordan changed his mind many times on the matter. At first he was essentially correct in recognizing two species--one for rainbow trout and one for cutthroat trout (however, Jordan changed scientific names for the species at different times). In 1895 he classified all known western trouts as subspecies of a single species, but he recognized three full species and many subspecies in 1896. In the early 1900's Jordan
evidently became frustrated in his previous attempts at trout classification and he began to recognize every variety as a different species. By the time of his death in 1930 he recognized 31 separate species for various forms of rainbow, cutthroat, and golden trouts (the Gila trout, Apache trout, and Mexican golden trout were unknown to Jordan).

Unfortunately, Jordan's works were widely disseminated in the popular literature and they became the major reference source for matters of trout classification in the angling literature.

The fossil record has so far not been very helpful for making a contribution toward a better classification of living species, but the study of trout fossils to date has barely scratched the surface of the subject. Salmonid fishes represent a very ancient group whose origin may go back 100 million years or more. The living species retain some very primitive features in their skeleton and other anatomical parts. The oldest known "trout" is a fossil found in British Columbia and represents a species that lived about 40 million years ago. The most commonly found trout fossils in the western United States are of a genus named Rhabdofario that was common in Pliocene times from about 3 million to 10 million years ago. Rhabdofario, however, doesn't appear to be the direct ancestor of our living species of native western trouts. It is probable that the direct ancestor of the present native trouts of western North America had its origin in the Far East. Successive waves of invasion into North American waters at the end of the Pliocene and during the early Pleistocene periods may have led to the complete replacement and extinction of the predecessor species of Rhadbofario. Thus, although the family

Salmonidae has very ancient origins, most of the living species are of relatively recent origin in terms of geological time. This recent origin of the living groups of western North American trouts has not provided sufficient time for divergence to a point to cause hybrid sterility between the groups. This complete interfertility among all the groups of western trouts prevents the clear-cut delineation of species.

Modern technology allows the critical examination and comparisons of differences in proteins and enzymes, the products of the units of heredity or genes, and of the chromosomes of different forms of trout. However, we are still far from a "final solution" to the problem of the most correct system of trout classification. The new evidence only supports the old--all of the native trouts of western North America are closely related to each other.

The human mind craves orderliness and it is frustrating to many that we do not know all of the secrets of the details of ancestral origin of a particular group of trout. I believe it is quite appropriate, however, that the mystery and awe surrounding trout sensed by anglers also carries over into the realm of scientific study of their classification. Once we know everything there is nothing more to be learned. The fun has been removed from the game.

## IMPLICATIONS

My main objective for the writing of two separate books on western trouts is better trout management, especially better management of wild, native trouts. The technical volume covers much of the same subject matter as this work but with more depth, documentation and citations to assist professional biologists to learn more about our native trouts and to encourage more ambitious programs emphasizing wild, native trouts so that they might play a greater role in state and federal fishery programs. This present volume, written for anglers, is designed to stimulate interest in our native trouts and to serve as a source of information so that anglers and spokesmen for angler groups can become more effective and more articulate in their efforts to effect better fisheries management, in particular, a shift in emphasis from domesticated hatchery trout to wild trout in fisheries programs.

It would therefore be useful to review, synthesize, and highlight some of the points brought out in previous sections and discuss their implications to better fisheries management programs.

A major asset for increasing the influence of an advocate group is to have - broad base support--the interests of all fishermen. Fly fishermen are often sincerely dedicated individuals who have developed a true reverence for trout. Frequently, however, fly fishermen are vulnerable to being labeled as representatives of an elitist group that is antagonistic to the wishes of the majority of fishing license buyers. It was characteristic for Charles Ritz, who fished private waters, to write that he despised anyone who killed a trout. Such an attitude, however, will not win many friends, nor influence the right people who make the decisions on the management of public waters in America.

In 1978 the Oregon Department of Fish and Wildlife evaluated the response of 2271 fishing license holders to a questionnaire. Although such a sampling of the angling public can provide useful information, I have strong reservations concerning its influence upon the direction of a fishery agency. Questionnaires can be used as an excuse for lack of leadership that should be the responsibility of the agency. The policies and direction of a modern fishery agency should be based on scientifically sound principles. Consider the consequences if the type of treatment at a medical center was determined by a vote of the patients. The respondents to questionnaires generally are not sufficiently informed on a subject to make the most correct or most intelligent choice.

In any event, the Oregon questionnaire turned up some interesting findings. About $50 \%$ of the anglers wanted more emphasis on wild trout-but $75 \%$ favored increased production of hatchery trout. At least half of the respondents favoring more emphasis on wild trout must also have favored more emphasis on hatchery production without realizing any contradiction. Overall, almost half of the respondents preferred to fish with bait. However, of those who sent in additional comments, 23 wanted more fly fishing only areas, 13 wanted more catch-and-release areas, and 19 wanted more emphasis on preserving native fish stocks while 5 wanted to eliminate fly and lure only areas and 2 wanted less fly fishing and more bait fishing areas.

An example that demonstrates the need for a better informed public (and better informed biologists also) concerns the response of steelhead anglers. Of the steelhead anglers returning the questionnaire, $82 \%$ expressed a preference for increased hatchery production of steelhead.

This is understandable because half or more of the catch of steelhead in many of the fisheries consist of hatchery fish.

In the previous section I mentioned that for practical management purposes, different runs of steelhead should be considered as if they were different species because it is imporant that the different types of life histories be recognized and accommodated in a management program. I would go even further and suggest that every distinct run in each river be treated as if it were a distinct species. I discussed how the various races or runs of steelhead evolved these differences to more fully utilize the whole environment of a river system and how hybridization between races was avoided by homing instinct. Obviously, each race must have a survival advantage in its own specific environment (spawning, rearing, downstream mitigation, upstream migration of returning spawners) over a steelhead race that is not native to that river because each race has evolved "fine-tuning" in its life history over eons of time in its "home" river. The practical implication is that the offspring of native races will have a higher survival and return proportionately more spawners to a particular river than hatchery raised smolts derived from another river system. This fact has been demonstrated for more than 50 years of study on Pacific salmons and steelhead trout. This raises the question: does massive hatchery production of steelhead act as a major factor to cause the decline of wild, native stocks? Let's take a closer look at some actual data.

In the 1950's the state of Washington began a greatly stepped-up hatchery steelhead program, continually increasing the numbers of smolts released each year. However, the stocks of hatchery steelhead are
derived from only a few rivers. That is, only a few rivers are being stocked with steelhead native to that river--an important point to keep in mind when considering survival, catch, cost of contributing fish to the catch, and impact on the native, self-sustaining races in the rivers being stocked with "non-native" fish. Despite this massive hatchery production, the total Washington steelhead catch by the mid-1970's was less than it was in 1953 before large-scale hatchery production. However, the proportion of hatchery fish in the catch has steadily increased while the catch of wild, native steelhead has drastically declined. Undoubtedly, negative environmental changes can account for some of the decline in native runs, but not all of it. A research study by the Washington Game Department sheds some light on why wild runs decline under the impact of heavy stocking of hatchery ("non-native") steelhead. The Kalama River in southwestern Washington has one of the state's more popular summer-run steelhead fisheries. This summer-run is largely supported by the return of hatchery fish (about $68 \%$ of the run is hatchery fish and $32 \%$ "native," or fish from natural reproduction). The summer-run steelhead stocked in the Kalama River are from the Skamania hatchery and this hatchery stock was derived from crosses made between summer-run steelhead from the Washougal and Klickitat rivers. A variant form of an enzyme (AGP) occurs in $18 \%$ of the hatchery stock but in only $1.5 \%$ of the Kalama River summer-run deived from natural reproduction. This great hereditary difference in the frequency of a particular enzyme reveals that the hatchery fish are not producing offspring that survive to sexual matury. If the hatchery fish did make any significant contribution to natural reproduction and the subsequent return of adults from natural spawning, this striking difference in enzyme frequency between wild and
hatchery fish could not be maintained. Thus, there must be virtually complete failure of the hatchery fish to contribute to natural reproduction in relation to reproduction yielding fish that survive until they return as spawners. I would assume that on the spawning grounds wild fish and hatchery fish would spawn with each other indiscriminantly. This being the case, it does not take high powered mathematics to figure the chances of a hatchery fish spawning with a hatchery fish, a hatchery $x$ wild spawning, and a wild $x$ wild spawning if the ratio of hatchery spawners to wild spawners is $68: 32$. From the enzyme frequency data, the return of wild fish from natural reproduction must be almost entirely from the rare spawning combination of wild $x$ wild fish, and, by chance, this most desirable spawning combination occurs in only $10 \%$ of the spawning population of mixed wild and hatchery fish when more than two thirds of the population consists of hatchery fish. My interpretation of this data suggests to me that the present hatchery program to maintain summer-run steelhead in the Kalama River, depresses the effectiveness of natural reproduction by up to $90 \%$.

This same research study on Kalama River steelhead genetics could not find any real differences in the enzymes between summer-run and winter-run steelhead in the Kalama--which is not at all surprising as I have already pointed out that summer-runs, winter-runs, and resident populations in the same river are very closely related to each other and it is not likely that significant differences would be found when examining the products of only a few units of heredity (genes) out of a total of 100,000 or more.

When some of the results of the Kalama River steelhead research were
published in a fisheries journal in 1980, I was amazed to read that the major conclusion of the study was that there is probably no hereditary differences between summer-run and winter-run steelhead in the Kalama River (which, to my mind, is nonsense--the differences in the timing of the runs can not be maintained without a hereditary basis) and therefore the present steelhead management policy of separate status for summer-run and winter-run stocks should be reevaluated. This is an example of a well conducted, sophisticated research project designed to uncover some answers concerning the causes of steelhead decline, but the conclusions drawn from the study, I believe, are simply wrong. There is certainly a hereditary basis for the different life history characteristics of summerrun and winter-run steelhead and this must be recognized for proper management. The main conclusion I draw from the Kalama River research is that the stocking of hatchery steelhead is the major cause suppressing the effectiveness of natural reproduction of wild fish.

In the Deshutes River, Oregon, a steelhead research project crossed wild $x$ wild, wild $x$ hatchery, and hatchery $x$ hatchery fish. In the hatchery environment the hatchery stock grew and survived better than the wild stock, but in the natural environment the wild stock was clearly superior to the hatchery stock in growth and survival. In the Gualala River, California a stocking of 20,000 non-native hatchery smolts from the Mad River hatchery returned about 100 spawners two years later in a run of 7,500 steelhead (that is, about 7,400 wild and 100 hatchery fish). Moreover, almost all of the Mad River hatchery fish return at three years of age whereas most wild steelhead in California rivers return at age 4 or 5. Thus all "trophy" steelhead of about 32 inches or more are wild fish.

These are the kinds of facts and figures that dedicated steelhead anglers should be made aware of. Once properly informed, I doubt that $82 \%$ would continue to endorse "increased hatchery production" as the highest priority program for increased steelhead abundance and improved angling quality. Well informed anglers armed with the pertinent facts and figures can influence administrators, commissioners, and legislators to at least make steelhead hatchery programs more cost-effective and demand a shift in emphasis to maximize the production of wild, native races. The future trends of our steelhead resource will not be determined merely by increased hatchery production or, in the long run, really much influenced by restrictive regulations to reduce angler kill. These are ancillary issues secondary to the primary goal of preserving and enhancing a diversity of native populations in high quality, natural environments. Such an issue is too important for an advocate group to lose much of its effectiveness from bickering over fly fishing versus bait fishing.

The subject of restrictive fishing regulations has long been dear to the heart of many fly fishermen. The notion that we can have many more and much larger trout in every fishery if only all or most of the trout caught were returned to be caught again is cherished by many anglers. The subject of special regulations is charged with emotion but typically slogans such as one commonly attributed to Lee Wulff--"a trout is too valuable to be caught only once"--are substituted for fact and reason. The conflicts between anglers and the professionals of a state fishery agency are not all due to ignorance on the part of the anglers. I find considerable ignorance among professional biologists on the subject of
special regulations and I have published some papers on this subject in an attempt to enlighten fishery biologists. After trying out various kinds of reduced or no-kill regulations on trout fisheries all over the country for more than 45 years, it's about time we know more about the subject and resolve the conflicts between fishery agencies and anglers to everyone's satisfaction.

As discussed in relation to trout movement, a whole stream does not have to be set aside under special regulations. Sections of one mile or less are workable units for special regulations. Such sections should be carefully selected to minimize antagonism with bait fishermen. Stocking of hatchery trout can be continued in the standard regulation sections of a river and by having stocked and unstocked sections the concentration of hatchery trout and those who want to fish for them together in the same area will result in more efficient utilization of the hatchery product. Both groups--catch-and-release enthusiasts and bait fishermen can be accommodated and satisfied on the same river.

The fact is, however, that there are relatively few rivers or river sections where the trout population will clearly show a significant response to greatly reduced angling kill by an increase in numbers and average size. This is due to the fact that angling mortality is largely compensatory, not additive, to natural mortality, and the continual removal of fish from a population typically stimulates recruitment and production. That is, the more trout killed by anglers, the fewer that die from natural causes. Those trout that survive in a fishery subjected to moderately heavy angler kill generally grow faster and the continual recruitment of new yearclasses into the population compensates for the removal of older fish by the
fishery. Thus, the long term trend in numbers, biomass, and average size remains relatively stable.

Obviously, there is some point where angler kill can become excessive and where restrictive regulations would be necessary for maintaining older, larger fish in the population. Three major criteria determine the success or failure of special regulations to increase the abundance and average size of trout and increase the catch rate. These are: fishing pressure (quantified in hours of angling per surface acre per year), the species of trout, and the life history characteristics and growth rate of the trout.

Before a stream section is put under special regulations, something about the size-age structure of the trout population, its abundance and mortality rates should be known. The environment determines carrying capacity and growth rate. If virtually no trout reach a length of more than 10 inches in a certain environment, then a 12 inch size limit will simply not work to produce 12 inch trout.

A criticism of most previous special regulations fisheries is that they lacked the proper before and after data necessary to evaluate their effectiveness, or to provide the scientific basis to predict if reduced angler kill would benefit a particular trout population. For example, if a survey finds that the catchable-size trout in a population ranges from 6 to 16 inches and consists of ages 2 through 6 and they exhibit an average annual mortality of $50 \%$ per year, some calculations and assumptions can be made to predict if restrictive regulations would be effective. As mentioned, angling-induced mortality is largely compensatory to natural mortality. As a general rule-of-thumb, we can assume an $80 \%$
compensatory factor. Thus, where natural mortality would be $50 \%$ per year with no angling mortality, an angling mortality of $40 \%$ ( $80 \%$ of $50 \%$ ) can be inflicted on the population without increasing the total annual mortality (= angling + natural mortality). In such a situation it can be assumed that an annual angler kill exceeding $40 \%$ of the catchable-sized trout will cause overexploitation and the population would benefit from restrictive regulations. The question then is: how much fishing pressure does it take before fishermen kill 40\% of the catchable-size trout each year under normal regulations? The answer depends on many variables such as the degree of expertise of the fisherman and the openness or fishability of the stream. The most important variable, however, concerns the species of trout. Brown trout are enormously resistant to overexploitation and a brown trout populaton will not favorably respond to restrictive regulations unless the fishing pressure is extremely high--on the order of about 500 hours per acre per year or more that might be characteristic of a trout stream near an urban center. There are brown trout fisheries such as in the South Platte River near Denver and Convict Creek, California, where special regulations have worked to greatly increase the abundance, average size, and catch-rate, but these fisheries are subjected to great fishing pressure ( 2000 to 3000 hours per acre on the South Platte and 3800 hours per acre per year on Convict Creek). In the past, hơever, the only response of a fishery agency to urban area fishing pressure intensity has been to plant large numbers of catchable-size hatchery trout. The results from the special regulation studies on the South Platte and Convict Creek reveal that trout can maintain maximum abundance and provide an excellent quality fishery with virtual unlimited fishing pressure if all or most of
the trout caught are returned and recycled in the catch.
In contrast to brown trout, the cutthroat trout is extremely vulnerable to angler catch in streams. Studies have revealed that only 12 to 20 hours per acre fishing pressure can catch $50 \%$ of all catchable-size cutthroat trout. Special regulations will more likely succeed with cutthroat trout than with any other species. After many years of failure or inconclusive results with special regulations all over the country with brown, brook, and rainbow trouts, the first clear-cut evidence that special regulations (no kill or very limited kill) could work to dramatically increase the abundance and average size of trout were with cutthroat trout fisheries in Idaho (St. Joe River, Kelly Creek) and in Yellowstone Park (Yellowstone River). The facts and figures were indeed startling--2 to 10 fold increase in numbers and biomass of catchable size cutthroat, 5 to 30 fold increase in large fish ( 12 to 15 inches and larger) after the restrictive regulations were imposed. The quality of these cutthroat trout fisheries has so vastly improved that they now support more angler use than before the restrictive regulations were instituted. This refutes the common belief that restrive regulations will always cause a decline in fishing pressure. It is true, however, that if restrictive regulations do not result in an improvement in the population then angler use can be expected to decline. In the past, special regulations have largely been applied in a haphazard manner in response to local agitation or political pressure, without consideration of the biological factors and quantity of fishing pressure that determines relative success or failure. Under such circumstances the entire concept has developed a generally unfavorable reputation among fishery agencies--
but the blame ultimately can be associated with a lack of expertise and lack of leadership in the agencies themselves.

The term "catch-and-release" does not necessarily denote a "no-kill" regulation. Minimum, maximum, or "slot" limits require that all fish below, above, or in between certain sizes must be released. Strict no-kill regulations are seldom the "best" type of regulations. They do not allow "fine tuning" of a population by harvesting a portion of the population to benefit growth and survival of the rest of the population. Each particular environment determines recruitment, growth, and age-size distribution of a trout population. Special regulations should be designed to optimize these parameters for the benefit of the trout population and for higher quality angling. This is a complex matter and requires considerable biological expertise on the part of agency biologists.

An additional complexity is when two or more species of trout occur in a special regulation area. Because of the differential vulnerability, the brown trout will be favored over other species under standard regulations, but a change in species dominance might occur when the factor of selective kill is removed. For example, in the Lewis River in Yellowstone Park the ratio of brook trout to brown trout was about 50/50 for many years under normal regulations that allowed anglers to keep some of their catch and the catch was 90\% brook trout ( $10 \%$ brown trout). In 1974 this section of the Lewis River was put under no-kill regulations. By 1978 the brook trout became overwhelmingly dominant over the brown trout--90\% to $10 \%$ because the differential angling mortality factor had been eliminated. This, in turn, lowered the quality of the fishery because now anglers catch virtually no large brown trout.

In the South Platte River near Denver, a section open to standard regulations and stocked with hatchery rainbow trout has about $30 \%$ rainbows and $70 \%$ browns. A neighboring section under no-kill regulations has about $70 \%$ rainbow and $30 \%$ browns (the no-kill section also has 17 times more trout over 15 inches than the standard regulation section). The environment in the South Platte actually favors rainbows over browns but under the intense fishing pressure of about 3000 hours per acre per year, the differential angler kill of rainbow trout makes the brown trout the dominant species. This dominance is reversed when angler-induced mortality is eliminated or greatly reduced and the population dynamics of both species are governed only by natural mortality.

These examples suggest that special regulations can be aimed at favoring one species over another. For example, where native populations of brook trout in the East or cutthroat trout in the West are threatened by brown trout, no-kill regulations can be applied to the native trout only, while allowing the harvest of brown trout.

A research study on the rare Arizona or Apache trout made by the Arizona Cooperative Fishery Research Unit demonstrated the differential vulnerability of our native western trouts in a fishery with brown trout. Two stream sections were sampled with electrofishing gear. The brown trout outnumbered the Apache trout by $20: 1$ in one area and by $4: 1$ in the other. Angling during daylight hours produced a catch of 55 Apache trout to 4 brown trout. These results suggest that the Apache trout is about 100 times easier to catch than the brown trout when they live together in the same stream. Even light angling pressure will act to strongly favor the brown trout and a no-kill regulation for native trout
only should be beneficial to correct this imbalance.
For any type of regulation where a significant part of the catch is released to be recycled in the fishery, angling must be restricted to fly and lure only to reduce mortality of the fish released. There have been numerous studies made on survival of trout caught and released on various types of flies, lures, and baits. There is great variation depending on many factors such as water temperature and if the experiment was conducted in a natural environment or a hatchery pond. In general, however, trout caught on bait can be expected to suffer about a $40 \%$ mortality after release. The survival of trout caught on flies and lures and released ranges from about $90 \%$ to $98 \%$ and will generally average about 95\%. No consistently significant differences are apparent in survival rates of trout caught on flies or hardward lures or on single versus treble hooks, or on barbed versus barbless hooks. Typically, trout caught and released with large treble hooks have extremely high survival because almost all deaths are due to the hook being swallowed and rupturing the respiratory filaments of the gills. Large treble hooks are rarely swallowed. Thus, the type of artificial fly or lure is not critical to the survival rate of released fish. There is no real justification for a barbless fly only restriction, and more general support for special regulations can be expected if discrimination against a significant segment of license buyers can be avoided.

How many times can a trout be caught and released? With brown trout in Convict Creek, each individual was caught-and-released an average of three times in a year when the fishing pressure was 3800 hours per acre. Rainbow trout in a no-kill section of the Frying Pan River, Colorado,
also were caught and released an average of three times a year, but at only a fraction of the fishing pressure of the Convict Creek fishery. Some individuals are "dumber" than others and are caught many times. Many of the rainbow trout in the Frying Pan River were tagged with identifying numbers. Mr. Bill Fitzsimmons, an excellent angler who lives on the Frying Pan River and fishes it regularly, recorded his catch in 1980. The last time I talked with Bill, in late summer, 1980, he, or someone fishing with him, had caught and released one particular rainbow trout 13 times--and always took it from the same site. Thus, there is no question that trout can be caught and released again and again.

A private fishery on the River Test, England, requires that every trout caught must be killed. The historical belief is that a released fish will learn from its experience and never be caught again and will become an old cannibal to the detriment of the fishery. Ancient British traditions are not susceptible to change by facts of experimental evidence.

I have no doubt that special regulations designed to recycle most of the catch will become a more significant part of fisheries management programs of the future. The number of people fishing in the United States has about tripled since the 1940's while the miles of quality trout streams have significantly declined due to dams, channelization and other conflicting uses of water. At the same time, the number of fly fishermen with a decided preference to fish for wild trout in streams has probably increased at a more rapid rate than the increase in anglers in general (based on the surge of literature devoted to fly fishing in the 1970s). The demands of this growing group of anglers dedicated to wild trout fishing cannot be satisfied by increased stocking of domesticated
hatchery trout. It seems obvious to me that various types of special regulation fisheries recycling the catch are the only way to maintain high quality wild trout fisheries under increasing fishing pressure. The amount of fishing pressure needed to make special regulations successful to achieve the objectives of higher catch rates and increased survival of older, larger trout will vary greatly depending on the species of trout, the "fishability" of the stream, the environment determining growth and natural mortality, and the degree of expertise of the anglers. Some cutthroat trout populations would greatly benefit from a highly restricted angler kill at only 10 to 20 hours per acre per year of fishing pressure, whereas little or no improvement might be found by reducing angler kill on a brown trout population subjected to more than 500 hours per acre per year of fishing pressure.

There is much yet to be learned about the effects of special regulations and fishery agencies should give a high priority to gather the necessary data to insure the success of special regulations to achieve the desired objectives. I was disturbed to read that the Pennsylvania Fish Commission declared a moratorium on new special regulation waters until they find out what they want to accomplish. I once wrote in a paper on special regulations that it was about time that the Pennsylvania Fish Commission decided what they want to accomplish with special regulations (they pioneered the fish-for-fun concept or the "Hazzard Plan" in 1934) and, to me, the idea of a moratorium on special regulations in a time of need is analogous to a moratorium on cancer treatment until a sure cure is found.

Special regulations will certainly play a larger role in the future
of wild trout fisheries, but regulations can not increase the abundance of trout beyond the carrying capacity of the environment. I have pointed out that the most significant area of emphasis for enhancing the future of wild trout will be measures that will increase the carrying capacity of the environment. This is possible from better livestock grazing management and better timber management that protects riparian vegetation and reduces erosion. Better flow and temperature regimes from dams and water development projects designed to favor trout are needed. By improving the cold water environment that has been degraded from past multiple use conflicts, many additional millions of pounds of wild salmonid fishes could be naturally produced annually.

An indirect method to enhance the quality of wild trout stream fisheries is to increase the quality of lake and reservoir fisheries. Most license buyers are rather labile in their fishing preferences. If good fishing exists in lakes and impoundments, the pressure is eased on streams and this results in lessening the demand for more stocking of streams with hatchery trout.

Fishery agencies should maximize the quality of both warm-water and cold-water lake fisheries to diversify angling opportunity. In lakes with a trout fishery potential, increased production can be achieved by taking advantage of the principle of ecological segregation and stocking two or more species or forms of trout to more fully utillize the resources.

In lakes where survival and growth of domesticated hatchery trout fingerlings is extremely poor due to competition and predation of other fishes and from marginal temperature regimes, experimentation with various wild races of trout that are "preadapted" to cope with such environments offers a
tremendous potential. The stocking of lakes with sterile fingerlings can greatly increase the total biomass caught by anglers because all energy would go into growth and the life span would be extended.

In warm-water environments characterized by an abundance of nongame fishes and few game fishes, innovative experimental stocking might be tried with hybrid combinations such as striped bass $x$ white bass and muskellunge x northern pike along with special regulations designed to maintain optimum predator density to create attractive fisheries and stimulate increased angler use of such waters.

Is your state fishery agency too burdened with a massive hatchery program to be able to assume a leadership role in these areas of progressive fisheries management? Are they effective in presenting a well documented case for maintaining and enhancing the aquatic environment in confrontations with conflicting uses? Are there specific policies and action programs to protect and enhance native trout and wild trout fisheries? How effective are they? Are data maintained on cost-benefit ratios of the hatchery program? How many pounds stocked, how many pounds caught, and what is the cost per pound of trout caught in each fishery? Is there a policy on what waters will be stocked? Are waters being stocked where the return of catchable trout is less than $50 \%$ ? Is there a negative impact on wild trout from any of the stocking programs? Does the hatchery program utilife wild races of trout for specific purposes and to improve fisheries where domesticated hatchery strains give poor results?

There is much to criticize regarding the large-scale stocking of catchable trout. They are expensive and detailed studies in Colorado and California reached similar conclusions that $8 \%$ of the anglers catch
$50 \%$ of all catchable trout caught. A small group of 1 icense buyers are highly subsidized by the majority. A return of $70 \%$ of a stocking of catchable trout is generally considered as good, but would anyone invest money and consider it a good investment to get back $\$ 7$ for every $\$ 10$ invested? Catchable trout stocking, however, can be used as an effective method of "crowd control" by concentrating anglers in certain areas and to create high intensity fisheries near urban areas. I do not envision a general phasing out of catchable trout stocking but a catchable program should be made as effective as possible by eliminating wasteful stocking and maximizing catch and use. Catchable programs should complement not conflict with wild trout fisheries. The costs and manpower involved with catchable programs should not be so burdensome that an agency lacks the funds and expertise it needs to carry out its primary function of preserving and enhancing the aquatic environment.

