

Datus C. Proper  
1914 N. Johnson St.  
Arlington, VA 22207

Feb. 21, 1987

Mr. Robert A. Bachman  
Rt. 1, Box 243  
Recovery Drive  
Centreville, Md. 21617

Dear Bob,

Thanks for the splendid portrait of Beethoven. I enjoyed figuring out the dot sequence. The picture could certainly have been taken on Thompson's, and I hope you'll have a chance to do similar photography there one day.

My impression is like yours: the trout in Thompson's act like yours in Spruce Creek. There may be a couple of exceptions.

1. Some of the lies change from year to year, simply because the weeds change. A number of pools are formed by chance as the plants grow, and of course the fish adapt. This doesn't apply to the pools controlled by permanent features, of which there are several. (I hope there will be more as soon as I can get in some stream improvements. Next summer I'll be looking for a cheap way to do that. Want to try logs secured by iron bars, but if you have seen any better ideas, please let me know.)

2. I haven't figured everything that happens in late fall and winter. Some of the trout stay around, apparently using muskrat holes for refuge. There is a shortage of good winter holding cover, and stream flows are low at the time. Before that, during the browns' spawning season, I may get some migrants up from the East Gallatin. One fellow swears he saw a 30" brown in late fall, and I'm not aware of any that big in the summer. Could be, though -- a 7-pound fish was taken on an artificial grasshopper a few years ago.

When I get a chance to spend the season on Thompson's, I'd like to do some tagging or fin-clipping to help settle these questions, and to find out how often the fish can be caught. As you discovered, they get awfully spooky. By late August they were nearly unfishable on bright days.

I haven't been fishing in Maryland for years and probably won't try it again unless you find something good. Believe I mentioned that Big Hunting Creek seemed poor to me even twenty years ago, before the dam. Went nearly stagnant in the summer, and in the spring the trout were all stocked. The Shenandoah streams were a pleasant contrast when I discovered them.



ROBERT A. BACHMAN  
241 SOUTH PENNSYLVANIA AVE.  
CENTRE HALL, PENNSYLVANIA 16828  
814-364-9983

January 28, 1986

Dear Datus,

Thanks for the opportunity to review your manuscript on "The Best Thing About Trout". I like the way you think! It's good.

I hope you didn't get the idea that I was getting too picky, but I wouldn't be doing you any good if I just said it's great. (But it is.)

There is still a lot we can all learn about how and why trout do what they do. Selectivity is, no doubt, one of the most fascinating things about trout, and I'm not sure we will ever figure it all out. But it sure is fun trying.

Hope to see you this summer some time. Ever fish the Delaware? It can be dynamite in the spring!

Cheers.

*Bob*

Bob Bachman





Bob Dackman

Datus C. Proper  
1914 N. Johnson St.  
Arlington, VA 22207

2/22/86

Dear Bob,

Thanks for your letter of January 28 and for your help with my manuscript on selectivity. I made a number of changes after our talk. After some thought, I did leave in the passage about the trout's large mouth, but I changed it somewhat and made clear that I was offering an opinion which which biologists might disagree. I also referred to the mouth later on, in another connection. Photocopies of both these passages are enclosed. No action needed -- just didn't want you to think I had ignored your comments, when and if you see this in Trout magazine.

It may be that the grayling is in fact a more efficient insect-feeder than the trout. Some of the British seem to think so, at least; I don't know. The grayling do seem to fill a niche in the chalkstreams that is similar to the Rocky Mountain whitefish in Montana. Both are fish that look insectivorous to me. I was surprised to find myself agreeing (after fishing the Itchen for a while) that the grayling needs to be kept down in numbers.

I was glad to have the full version of your paper on foraging behavior. I had read the simplified version of it in the magazine. Found it a welcome relief from assertions by fish-writers over the years that trout get most of their food off the bottom. I don't know who first said it (Hewitt?), but it has certainly been repeated without thought too often.

Also enclosed is a copy of an article from The Field. It appears to summarize some really interesting research. Among other things, it seems to support a thesis of my book, which is that trout pay more attention to the behavior, size, and shape of a fly than to its color. If you know where I can get the paper this was based on, I'd appreciate a reference.

Thanks again.

Yours,

Datus



Robert A. Bachman  
Rt 1, Box 243  
Recovery Dr.  
Centreville, MD 21617

Feb 8, 1987

Mr. Datus Proper  
1914 N. Johnson St.  
Arlington, Virginia 22207

Dear Datus:

I can't tell you how much I appreciated the fishing on Thomson's Creek last summer. That is a fabulous resource. I had a great time, because those are some of the toughest fish I've ever tried to catch. Not because they were "selective", but because they were so hard to approach without spooking. Of course, it didn't hurt to find that when I watched them, they behaved exactly the way my trout at Spruce Creek behaved. In addition to having fun, I learned a lot.

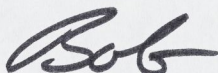
I told you most of the details of my fishing. When I was there in July, the fish were feeding mainly on pale morning duns. It seemed that they would readily take a reasonable approximation if I could present a drag-free drift to an unalerted trout. But, as you know, that is no small challenge there. I used the heaviest tippet I could with the size fly I used, and that usually meant 6X. The only fish I broke off was the big bank-sipping brown, but that was my fault. If I had been using my 2 weight, I might have had better luck.

It was after I left your place, and had fished on the Madison and the Big Horn that I realised what a nifty piece of equipment that 2-weight rod really is.

Enclosed is a photograph of one of my trout at Spruce Creek. (Beethoven). Thought you might like it.

I still hope to meet you before too long. If I find time to get in some quail hunting I'll be sure to get in touch, but February is fast slipping away.

Cheers!



Bob





1883-1983

BROWN TROUT

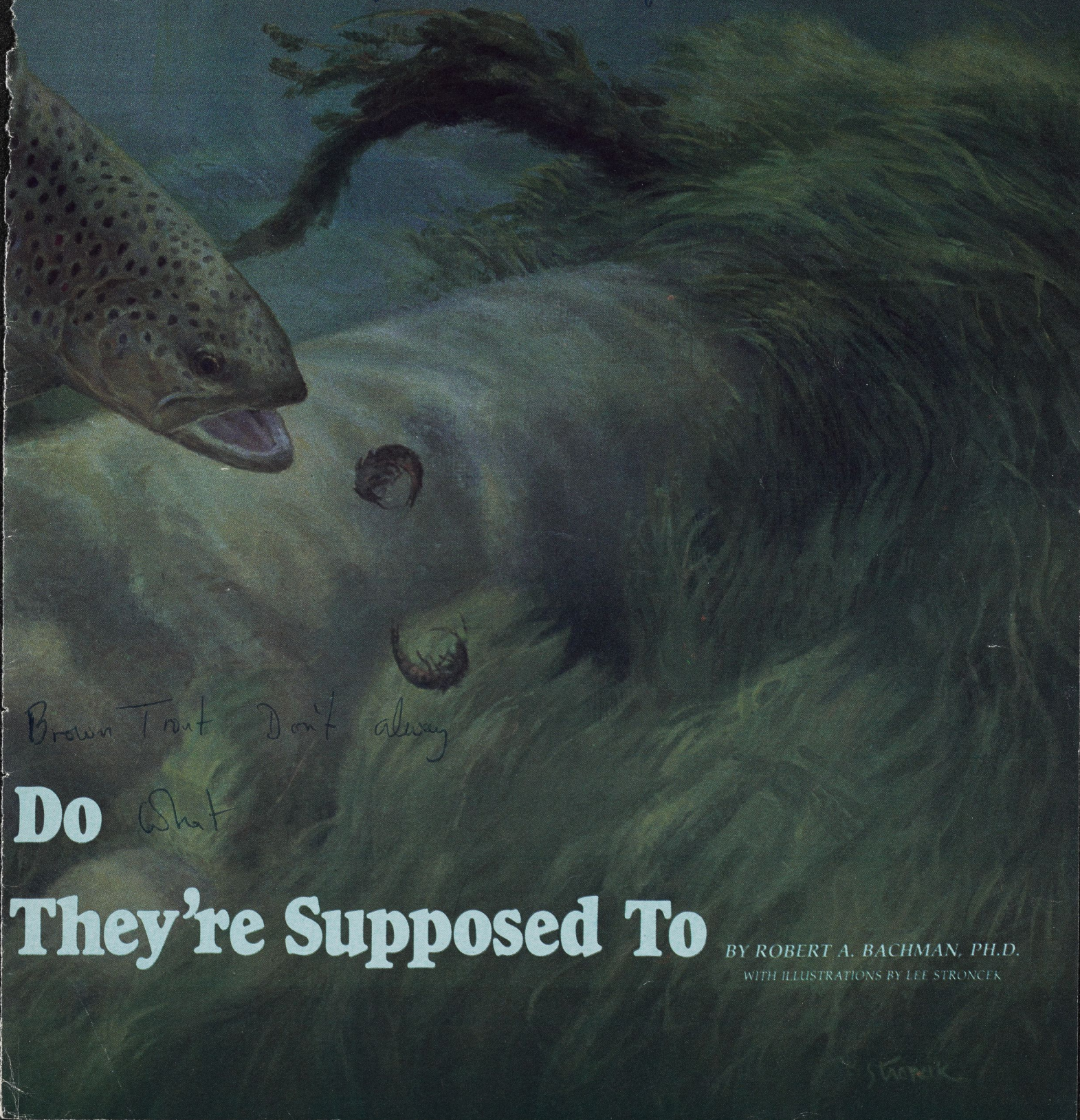


IN AMERICA

100 Years

— Why Dries often work better  
than nymphs.

— Brown seldom get over 14", even in fertile stream.



Brown Trout Don't always

**Do** What

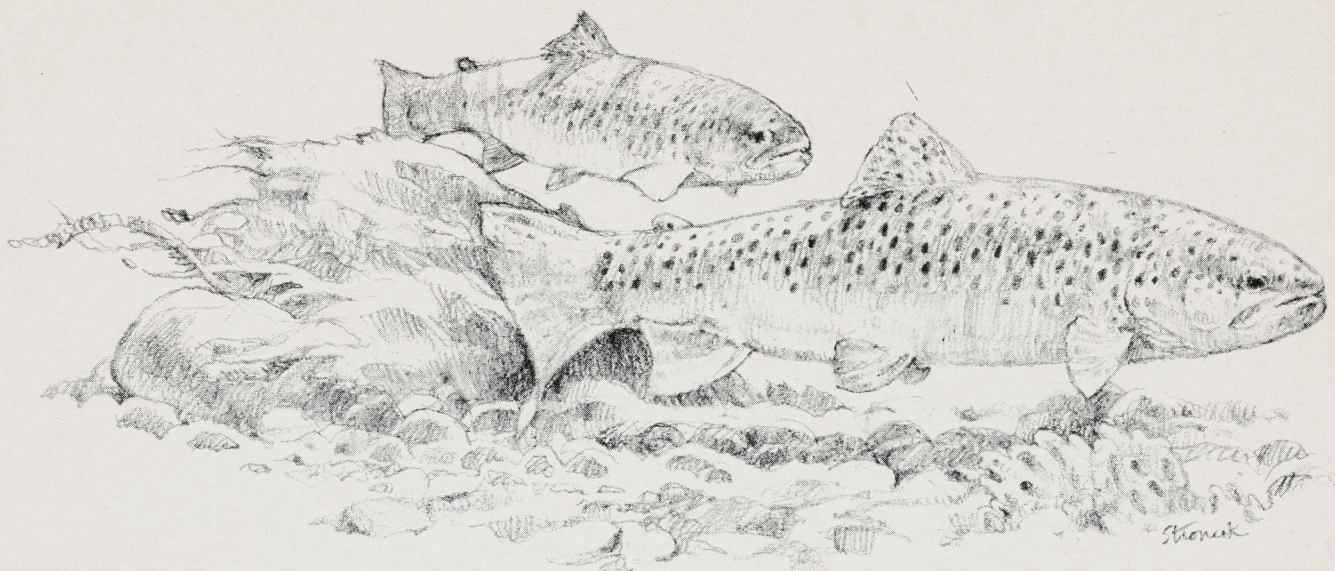
**They're Supposed To**

BY ROBERT A. BACHMAN, PH.D.

WITH ILLUSTRATIONS BY LEE STRONCEK

Stronck





**T**HE STREAM BELOW ME was alive with yellow-bellied, red-and-black-spotted trout, their dorsal, pelvic and anal fins delicately outlined in white. The distinctive black spots, set off by a light halo, and the red edging of the adipose fin told me they were European brown trout, *Salmo trutta* L., now as American as MacDonald's and Stroh's and frankfurters and scotch.

Only days before I had been walking the banks of Spruce Creek in Pennsylvania, half-heartedly looking for a place to set up observation towers from which I hoped to learn something about trout behavior. Professor Robert L. Butler, my thesis adviser, had suggested that I "study" trout by watching them from towers. When I first saw Spruce Creek my heart sank. The banks were lined by a thick growth of brush and overhanging grasses, and many of the pools and riffles were edged with snags and log jams. I wondered whether Dr. Butler was a trout fisherman. If so, perhaps, like many other anglers, he had fished only for hatchery trout. Didn't he know that wild trout stay hidden under rocks and undercut banks, or in deep, turbulent water? Or that they only venture out into shallow water at dawn and dusk, or when the stream is muddy?

As I walked up and down the banks of this section of Spruce Creek, owned by the Pennsylvania State University, I repeatedly crossed the stream at the tails of pools. Each time I crossed I spooked what appeared to be a few small trout. Since the water surface was relatively flat and calm, and since it appeared that at least a few small trout were present, I set up my first observation tower among some honey locusts near the tail of a large pool. I was totally unprepared for what I saw the next day. My years of fly-fishing for trout, and the litany of the angling fraternity, had convinced me that brown trout, especially wild brown trout, were shy, reclusive creatures. But here were dozens of brown trout feeding in the bright July sunlight, clearly visible to me from my vantage point some ten to fifteen feet above the stream. And they were not just fry and parr. Most of them were eight to twelve inches long. Butler was right. I really *could* study wild brown trout without handling or constraining them!

I spent the better part of the rest of that summer working out how best to observe the trout, what data to record, and how to record it. I would like to say that it was easy and the ideas were all my own, but that is not how science works. For example, my most valuable tool, a huge old 400mm telephoto lens borrowed from the still photo lab of Penn State was originally brought out to Spruce Creek by Mark Corneal, an undergraduate student who first helped me with the observation towers and other "forced labor." Another student, Mark Gammernan, came up with the idea of using video equipment to record the movement of the fish.

**M**any of those first days were spent just watching. Like many other anglers, I had often seen trout from bridges, or caught short glimpses of trout while approaching a stream bank in deep grass or brush, but I had never really concentrated on the same part of a stream for days at a time. After the first two or three days I was fairly sure that I was seeing many of the same trout each day, but I did not know how I could be certain. Other scientists had identified individual animals by more or less permanent marking such as nicks and scratches on the dorsal fins of dolphins. But these trout were mint perfect!

Nevertheless, certain individual fish gradually became more and more familiar to me. The trout were quite motionless for fairly long periods of time, and I was observing them through eight-power binoculars, so I could see them quite well. Suddenly it hit me! The black spots formed distinctive shapes like constellations of stars, and each one was quite different. I had found a method of identifying individuals, but now had to be able to demonstrate that it would work consistently. The 400mm telephoto lens was the answer.

I started taking photos of every trout I could find and naming them. One, a particularly colorful fellow with bright yellow pectoral fins I called, not very originally, "Yellowfin." Another acquired its name from its spot pattern in the shape of the Greek letter *Lambda*. Still



another had three spots in a straight line followed by a space and then another spot. By this time I was assigning the fish numbers and this one was named "Thirty-One." He was later also known as "Beethoven" because his spot pattern reminded one observer of the famous da-da-da-DUM of Beethoven's Fifth Symphony. In all, in four years of observations at Spruce Creek, I identified nearly one hundred different trout. Photographs showed that the spot patterns remained unchanged as the trout grew over the four years of observation.

Within the first few days I realized that the same trout were using the same feeding sites day after day. They sat in front or on top — but always on the downward-sloping rear surface — of a rock or other submerged object. From these "lies" the trout would dart to intercept food items drifting by on the surface and in the water column. Each time a trout left such a lie or feeding site, the current would begin to sweep it downstream. Immediately after the nymph or mayfly was intercepted, the trout would quickly work its way back upstream, keeping near the bottom, where the current was weaker. Only occasionally would a trout spot and take something off the bottom.

I noticed that the position of the trout when in the feeding site had a precision measured in fractions of an inch. It was quite apparent that the trout chose lies in places where they were protected from the current but at the same time had an unobstructed view of food drifting downstream to them. I could see, for example, that when a trout was in its lie very little effort was required to maintain its position in the stream. It took only a slight movement of the pectoral fins and a flick of the tail to propel the trout into the slipstream to intercept food. The stream was acting like a conveyor belt, carrying food to the waiting trout.

The precision of the feeding sites also provided a reference for measuring the home range of individual trout and the location of feeding events and other activities. Typically, each trout used from six to ten feeding sites within an area of approximately 150 square feet, although the majority of the time was spent in only three or four such sites. The area in which a trout spent most of its time, its home range, frequently overlapped the home range of its neighbors by a considerable amount. In fact, the home range of one trout might be completely contained within that of another. It was not unusual to find two or more trout using the same feeding site sequentially throughout the day. However, no two trout ever used the same site at the same time.

Whenever a trout in a feeding site was approached by another trout a fight or "agonistic encounter" was likely to ensue. The winner of such a contest was usually the larger of the two. It was quite apparent that neighbors could recognize each other, for the smaller of the two would retreat or give way to the larger with little or no contest. But trout of equal size, and strangers, were much more likely to engage in protracted and energetically taxing contests. The result of these agonistic encounters was a fairly rigid "pecking order" or dominance hierarchy which remained remarkably stable from year to year.

Despite the abundance of snags, undercut banks and overhanging vegetation, it was a rare occasion

when I could not find a trout I wanted to observe. I could see less than one fifth of the total area of the pool from the observation towers, but I had better than a 60% chance of seeing any fish that I wanted to observe at any time of the day. Obviously the trout were not wandering all over the pool, but had very restricted home ranges and they rarely were hidden from my view from the observation tower. That is, they rarely were under what is normally referred to as "cover."

The trout typically responded to the overhead flight of a kingfisher, crow, grackle or other potential predator by a sudden dart to one side or the other and then

***"Obviously the trout were not wandering all over the pool, but had very restricted home ranges . . . they rarely were under what is normally referred to as 'cover'."***

pressing their bodies tight against the bottom and remaining perfectly motionless. In such a configuration they were very difficult to see. In the absence of further fright stimuli the trout would usually resume feeding within a minute or two. Stronger stimuli, such as the approach of a human, or repeated short stimuli, resulted in a wide dash for the nearest brush pile, undercut bank or space beneath a rock. In such rare cases the trout normally did not return to their feeding sites for at least twenty minutes.

**T**he trout in Spruce Creek rarely, if ever, got enough to eat. Although Spruce Creek is a highly productive, very fertile stream, the trout were always feeding. There was never a time from dawn to dusk, from April through October when the trout were not feeding. To be sure, the feeding rates varied greatly from hour to hour and day to day, but in the long run there was little difference in the feeding rates from one hour to the next, except for short flurries of activity at dusk in May and June during the evening sulphur hatches and spinner falls. Even when "Beethoven" downed two huge crayfish within the space of about twenty minutes his ravenous appetite was little affected. He went right on picking off mayflies and caddisflies as though he hadn't had a thing to eat for weeks.

As I mentioned, the trout took a relatively small quantity of food off the bottom. Less than 12% of the more than 15,000 feeding events I recorded involved bottom feeding, even though practically every rock in Spruce Creek is covered by caddis, mayfly and stonefly nymphs. Most of these are not available to the trout. First of all, many of them are under the rocks and in the spaces between the rocks. Second, they, like the trout, are quite cryptic in coloration and are not easily seen. A trout can see only a small portion of the bottom at any given time from its feeding site less than a centimeter off the bottom. Items in the drift, however, even those which are submerged, are silhouetted against the sky and are therefore more visible than things on the bottom.

*why do flies work...*



The trout moved from one feeding site to another like marbles in a Chinese checker game. They moved immediately and directly from one discrete site to the next. Virtually no time was spent cruising the area in search of food on the bottom. The most probable explanation, it seems to me, is that the extra energy the trout might get by searching for food on the bottom would not compensate for the energy spent in continually fighting the current.

Occasionally the trout would rise off the bottom and remain stationary with respect to the bottom by swimming at the same speed as the current just beneath the surface, while sipping insects on the surface. This occurred only when there was a superabundance of food on the surface and only for short periods of time, usually less than fifteen minutes.

The trout spent *over 86% of their daylight hours* in a sit-and-wait search mode in feeding sites. An additional 8.4% was spent returning to the lie after pursuing and capturing food in the drift. That is, the second most time consuming activity next to searching the water column for food from the feeding site was fighting the current to get back to the lie. Just slightly over 3% of the time was spent actually pursuing food, which left less than 3% for all other activities such as agonistic behavior and moving about.

As the trout grew older they fed less frequently. For example, the average feeding rate of four-year-old



trout was only about half that of yearling trout. Once in a while I would see a younger, smaller trout feeding downstream and in sight of a larger trout. Invariably, the smaller trout was feeding at a higher rate than the larger trout. The large trout was passing up some food items that the smaller trout ate. I never, however, witnessed the converse: a smaller trout feeding upstream of a larger trout. Not within sight of the larger trout, that is. A small trout feeding — or attempting to feed — upstream inevitably elicited an attack by the downstream trout.

The photographs of trout in known feeding sites also afforded me a means of measuring their growth. The trout grew very rapidly during the first two years and then began to grow more slowly. They reached about half their ultimate length at the end of the first two years of growth, and few trout reached a length of twelve inches in less than five years. Yellowfin was the dominant trout in my observation area each year from 1978 through 1981. He was eleven inches long when

photographed in August 1977 and when captured in 1982 he was only slightly over 13 inches in length. Other mature trout experienced similar slow growth.

***“Food on the bottom contributes little to the trout’s diet simply because much of it is not available and what might be available takes too much energy to get.”***

I have attempted to describe what I observed in my four year study of a free-ranging population of wild brown trout in a productive, fertile stream. While each stream is different from every other, I think some general conclusions can be drawn from the behavior of the trout in Spruce Creek.

First of all, in order for a trout to grow it must obtain more energy from the food it eats than it expends in routine metabolism and pursuit of food. It appears to me that this necessity is reflected in every behavior exhibited by the trout I observed in Spruce Creek.

**F**eeding sites are chosen to minimize the energy expended in the time between feedings. It appears that in Spruce Creek the trout cannot tell where or when the food will become available. Otherwise the home range of individuals would not be so small and so stable from year to year. The best that a trout can do is find places in the stream, feeding sites, where it has refuge from the inexorable downstream pressure of the current and from there pick off food carried to it.

The precision of the sites demonstrates that the sites are chosen for their energy-saving characteristics rather than for the amount of food which can be obtained there.

The dominance hierarchy established by agonistic encounters between trout also functions as an energy saving mechanism. If two trout were both to pursue the same food organism at the same time only one would be rewarded. They don’t share mayflies. It is easy to see that in the long run the energy expended in agonistic encounters is more than compensated for by the savings brought about by spreading the population over all suitable habitat.

The fact that larger trout feed less frequently than the smaller trout is additional evidence that the trout are good at balancing their energy budgets. A larger trout must spend more energy to intercept food items in the drift than a small trout. As a result, there is less food available to larger trout than to small ones. Older (and bigger) trout gradually must eliminate the smaller food items from their diets. There is no point in spending energy chasing a food item that has in it less energy than it takes to catch it.

It must be stated at this point that it is not good enough for a trout just to get more energy than it expends. It must also try to do this better than its neighbors, because its reproductive success depends upon maximizing its rate of growth. If a fish does not feed at every available opportunity, another trout that



does is likely to have more offspring and more of its genes will be represented in the next generation. The bottom line for a trout is reproductive success. Trout must feed at every available opportunity. That is, they must feed at all hours of the day when they can see well enough to feed efficiently. They cannot afford to remain away from their feeding sites for long in places where the current would not bring them food.

As we saw, the food on the bottom contributes little to the trout's diet simply because much of it is not available and what might be available takes too much energy to get.

***"To you anglers who like to dredge the bottom with weighted nymphs, I can only remind you that the trout in Spruce Creek took less than 12% of their food off the bottom . . ."***

And finally, how can the knowledge gained about brown trout in this study be applied to the interests of anglers and fishery managers?

**C**over may or may not be important, depending upon the level of predation, but energy saving feeding sites would appear to be absolutely essential if a stream is to produce trout. We all know of food-rich sand and gravel streams which are relatively devoid of trout. An example is Big Spring, a well-known limestone stream in south-central Pennsylvania. Hundreds of yards of this stream are devoid of trout where the bottom consists only of sand and gravel, but wherever a few rocks break the monotony of the bottom there are trout.

Apparently trout rely on their inherent wariness as their first line of defense against predators and anglers. It follows then that trout which are in slow moving, clear water are much more difficult to approach and in heavily fished streams such places may be the only ones to hold trout by mid or late season. It is even more important to the angler to be especially cautious when approaching flat water in heavily fished areas. I rarely bother with fast or deep water after the hatchery fish are gone because I know there will always be plenty of wild trout in these hard-to-fish spots.

Trout eat constantly. They have to. For fishermen this means that while the short 20 minutes at dusk may be the most exciting (or frustrating?) the good angler fishes whenever he has time and appreciates the challenge of fishing when the odds are more in favor of the trout.

To you anglers who like to dredge the bottom with weighted nymphs, I can only remind you that the trout in Spruce Creek took less than 12% of their food off the bottom and moved a much shorter distance from their lies for bottom food than for food in the drift. It takes more casts to cover the same amount of

water with a weighted nymph because a trout usually cannot see things on the bottom at a distance of more than a few inches.

The most startling thing I observed at Spruce Creek was the large proportion of relatively slow growing old fish in the population. We have seen that the trout in Spruce Creek grew rapidly for the first two years, and then grew more and more slowly. And we have seen that in order for a trout to grow it must obtain more energy from the food than it expends getting it. We have also seen that a trout may spend most if not all of its entire life in an area not much larger than the average living room rug. Eventually, the trout grows to such a size that the energy it expends approaches that obtained and it stops growing. It takes only two years to raise an 8 inch trout in Spruce Creek, but it may take four or even five years for the average trout to reach 12 inches. Even under catch and release regulations fewer than 5% of the trout in most streams are over 12 inches. Most of the trout will never get to be 14 inches — regardless of how old they get.

Each stream will differ in growth rates and the maximum size that the drift-feeding trout will attain. But the shape of the growth curve of other streams does not appear to differ greatly from that of Spruce Creek, even where angling pressure is heavy. If this is so, it seems to me that the larger, slow growing trout must be protected to insure a quality sport fishery. We can't have our big trout and eat them too. A maximum size limit rather than a minimum size limit might be the answer.

In any population there are only a few large fish, and it takes a long time to grow them. So we've got to put the bigger fish back if we want to have big fish to catch. We used to say "If a trout is big enough to run the reel he is big enough to keep." Did we have it backwards? Might we not better say "If he runs the reel he's earned his freedom"?



#### References

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# Hey You!

To Our Fellow Members:

At last . . . we assume you've noticed . . . Chandler, Schwiebert, Whitlock . . . more pages, more color, more fishing, better content, better coverage . . . your magazine . . . *our* magazine . . . **Trout!!!**

One year ago, the National Board of Directors of Trout Unlimited gave us an assignment: Give our members more and better . . . make our magazine the rival of *any* sport fishing publication . . . research it, expand it, improve it; in short, give the members of Trout Unlimited the best bargain in the fishing world and, while you're at it, make **Trout** as fine-quality as any fishing periodical on the market.

What you have in your hands is just the beginning. It is the foundation for what will be the very best fishing magazine available. We've got a whole host of new ideas, a hell of a lot of enthusiasm, and the complete support of TU's Executive Committee. Now we need your help. Please take a few minutes today to fill out this important questionnaire. Let us know where we hit and where we miss; tell us what *you'd* like to see; send us your ideas and criticisms.

We even pay real American dollars for first-class articles, photos and artwork — some deal, huh?

There are a lot of people to thank for the new **Trout**. If you see them, pat'em on the back: Tom Pero, Jerry Schuder, Bob Herbst, Jim Gracie, Jean Bollinger, John Fritts, Sal Palatucci, and all the members of the TU Information & Education Committee — just to name a few.

In the future we'll be investigating more issues each year, expanded content, more superstars and newsstand distribution. It's all for us, the members of Trout Unlimited, and all for a low fifteen bucks a year.

So let's hear from you — from the Madison to the Penobscot, from the Chattahoochee to the Pere Marquette.

Charles W. Dibner, Chairman  
Information & Education Committee





## Maryland Department of Natural Resources

### Tidewater Administration

Tawes State Office Building  
580 Taylor Avenue  
Annapolis, Maryland 21401

William Donald Schaefer  
Governor

Torrey C. Brown, M.D.  
Secretary

February 21, 1989

Datus C. Proper  
1085 Hamilton Road  
Belgrade, MT 59714

Dear Datus:

Boy, do I envy that address! You have your priorities straight.

Thanks for the reference, and calling it hard information. That is what I intended it to be, and it is still gratifying to see it referred to as such.

I have enclosed a copy of the Transactions article, and in it you can readily see that a surface feed generated a "rise form". In fact, that was how I defined it. (See methods section, page 5.) Bottom feeds were defined as those times that the trout dislodged silt when it fed, or "bumped its nose" when it fed. It is hard to explain in the linear context of writing, but is exceptionally easy to describe with the aid of video tapes or cinematography. Figure 12, page 13 is based on over 32,000 individual feeding observations, in water depths ranging from six to 40 inches.

(406) 666-2320 (Good guide!)

You might want to talk to Jim Laughery, Fort Smith, MT. I have floated the Big Horn with him twice, and talked about brown trout behavior. He says the brown trout in the Big Horn act just like the ones in Spruce Creek. In fact, on our last float, he caught a snaggle-toothed brown and commented on how often he had caught that very fish, and that he could often count on that one to satisfy a client that wanted to catch a trout over 20 inches. If you consider the incredible numbers of trout in the Big Horn, and the size of the water, that sort of "stationariness" is extraordinary. And do they ever feed on the surface!

I can't resist making some additional observations on your article. (Obviously I like it.) I have at times described a brown trout as a fish that has evolved to capitalize on a very specific diet: a relatively helpless adult aquatic insect, loaded with high nutrient value--eggs. That is, I think, why flyfishing originated with trout fishing. And why trout fishermen are so crazy about flyfishing. I could go on!

Telephone: (301) 974-3061

DNR TTY for Deaf: 301-974-3683



Comment 2a. I believe I have actually seen some very old trout flies in a frame attributed to classical Greek times. I can't remember where I saw them, but it could have been the New York Anglers Club.

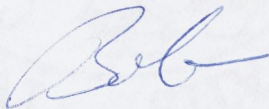
Comment 3. Are you, in a not-too-subtle way, suggesting that nymph fishing is just bait fishing, but with bait that doesn't smell/taste good? I've been known to think along those lines.

Comment 4. Selectivity can be viewed in two (at least) ways. First, as you use it, "hook shy". The other, and vastly more frustrating for me, is when the trout concentrate on just one species, usually a midge or trico, and seem to be blind to anything else. I believe they do it to feed more efficiently, as you may remember my comments on sharks, peanuts and popcorn.

Female browns usually mature by the end of their third year, males by the end of the second. I'd venture that the average age of the spawning population is about four years old. So it all depends on your math. I'd settle for three years for a generation, but I doubt that other than a quibbler would argue with you.

Hope this is of use to you. I'm delighted to hear from you, and hope to meet up with you next summer. I'm planning to attend the Wild Trout Symposium at Yellowstone in September, and spend at least some time fishing. I was in Montana last August, and had I known that you were out there, I'd surely have stopped by.

Sincerely,



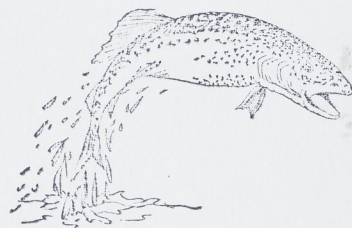
Robert A. Bachman, Ph.D.  
Chief, Freshwater Fisheries Program

RAB/sg  
Enclosure



Dates:  
May not all your trout  
be too subtle.  
Bob

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## Foraging Behavior of Free-Ranging Wild and Hatchery Brown Trout in a Stream<sup>1</sup>

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### Abstract

Wild brown trout *Salmo trutta* in a fertile, high-conductivity stream in central Pennsylvania were observed from camouflaged towers for three consecutive years in order to quantify the diurnal feeding and social behavior of undisturbed adults. The foraging behavior observed was characterized in general as one of net energy maximization effectuated principally by cost minimization. Individuals ranging in age from young of the year to 8 years spent 86% of foraging time in a sit-and-wait search state, used discrete, energy-saving foraging sites year after year, and fed mainly off drift, taking less than 15% of their food items directly off the bottom. Feeding rates decreased with age, were highest in spring and fall, and showed little effect of time of day except for short peaks at dusk in May and June. The home range of most individuals was established in the first or second year of life and changed little thereafter. The mean size of the home range of individuals was 15.6 m<sup>2</sup> and decreased slightly during the first 4 years of growth. No individual had exclusive use of any home range and no clearly defined territory could be described for any fish. Rather, the social structure evidenced is best described as a cost-minimizing, size-dependent, linear dominance hierarchy of individuals having overlapping home ranges. There was no apparent correlation between dominance and site selection with respect to distance to cover or feeding rate. Use of overhead cover ranged from 17% or less of daylight hours for wild brown trout of age-group 2 to no more than 43% for age-group 5. Length was asymptotic at 40 cm. A rectangular hyperbola described well the overall growth curve of fish in this population, half of the asymptotic length being attained at the age of 23 months. Hatchery brown trout, introduced for experimental purposes, fed less, moved more, and used cost-minimizing features of the substrate less than wild trout. It is postulated that high energy cost is a major cause of mortality among hatchery-reared brown trout stocked in streams, that at high population densities foraging sites are limiting factors, and that growth rate of drift-feeding salmonids is density-independent.

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Many of our ideas about the social structure and population dynamics of salmonids in streams

are based on studies of juveniles in laboratory conditions and spot samplings of natural populations (Northcote 1969; Butler 1974; Gerkling 1978). Few studies have included direct observation of undisturbed wild populations and those that have, have been qualitative in nature for the most part (Fabricius and Gustafson 1955; Newman 1956; Horton 1961; Keenleyside 1962; McCormack 1962). Recently, Jenkins (1969), Bassett (1978), and McLaren (1979) studied the

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<sup>2</sup> The Pennsylvania Cooperative Fish and Wildlife Research Unit is jointly supported by the United States Fish and Wildlife Service, the Pennsylvania Fish Commission, the Pennsylvania Game Commission, and The Pennsylvania State University.



social structure; Baldes and Vincent (1969) the microhabitat; Devore and White (1978) the response to cover stimuli; and Ringler (1979) selective feeding of wild brown trout *Salmo trutta* constrained in artificial or simulated stream channels.

Griffith (1972) and Fausch and White (1981) used mask and snorkel to observe wild trout populations in natural streams and to measure the microhabitat used by individuals, but, except for this study, I have been unable to find in the literature any quantified, long-term observations of the social structure and feeding behavior of unconstrained wild populations.

The density-regulatory effect of social behavior among salmonids in streams has received considerable attention (Chapman 1966; Chapman and Bjornn 1969; McFadden 1969) but remains somewhat equivocal. The regulatory mechanism generally invoked is territoriality, and despite (or perhaps because of) the lack of direct observational data, the concept of territoriality among stream-living salmonids is virtually dogmatic.

An increasing number of authors have begun to question the concept of territoriality, especially as it applies to the nonreproductive phase of stream-living salmonids. Allen (1969), in attempting to correlate territory size with the size of fish, remarked that he was able to find little direct measurement of territory size in the scientific literature. Jenkins (1969) reported that strictly territorial individuals were rare, and later (1971), in discussing territoriality, commented, "I find a simple, precise form of social density control difficult to visualize in such a social framework." Concerning the possibility of territoriality being an artifact of experimental design, Hoar (1969) warned, "... laboratory studies can be misleading as well as revealing in our attempts to understand the ecology of fishes." Butler (1974) described the behavior of salmonids in terms of a "social force field" (McBride 1964) and suggested that wild adult trout, in contrast to juveniles, had "no territory as understood in the traditional sense." Later, Ito (1978), in discussing territory stated, "Under special circumstances such as fish kept in an aquarium, the defense of an area observed will not constitute territoriality unless it has significance in the *normal* life of that species in the field." Noakes (1978), in commenting on the distinction between territoriality and domi-

nance-subordination relationships stated, "We must have individual identification of the fish within a group, and evidence that dominance is independent of location within the study area, before reasonably concluding that a dominance hierarchy is present." And, further, "We should exercise caution in ascribing consequences to, or even inferring the existence of territoriality without direct confirmatory observation."

A basic tenet of behavioral ecology is that animals behave as they do because the behavior in question enhances the reproductive success of the individual exhibiting the behavior (Pyke et al. 1977; Krebs and Davies 1978). That is, the behavior is adaptive. The interesting questions concerning adaptation often concern how animals respond to different aspects of the environment (Maynard Smith 1978). If we are to understand the mechanisms by which food and space regulate the growth and distribution of salmonids in streams, we need to understand how an individual animal responds to environmental variables in order to maximize its reproductive success. The purpose of my 3-year study was to acquire such understanding of an undisturbed population of wild brown trout and to analyze the extent to which such concepts as dominance and territoriality pertain to free-ranging populations.

A second objective of the study was to quantify the differences in behavior of wild and hatchery-reared brown trout and to investigate the possible causes of poor survival of hatchery brown trout in streams.

### Study Site

Spruce Creek is a hard-water stream rising from limestone springs near Rock Springs, Huntingdon County, Pennsylvania and flows generally southwest through farmland and hardwood forest for 15.5 km to its confluence with the Little Juniata River at the town of Spruce Creek. Fed by two major tributaries, Halfmoon Creek and Warrior's Mark Creek, it varies in width from approximately 5 m at its confluence with Halfmoon Creek to 12 m at its mouth. Although subject to flooding after severe summer thunderstorms and after winter rains when the ground is frozen, the stream drops quickly after such infrequent episodes, and has a fairly steady flow year round (McFadden and Cooper 1964).

In an ecological comparison of six brown trout



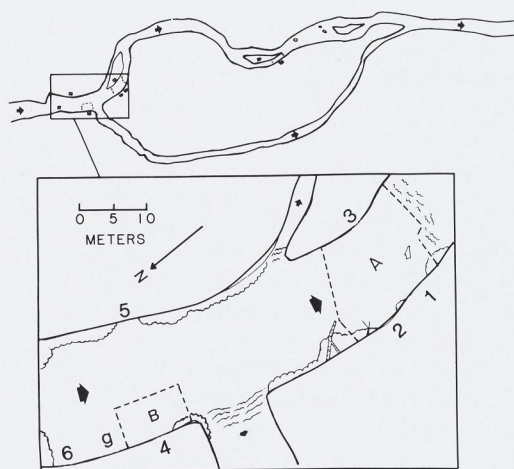


FIGURE 1.—The Spruce Creek Experimental Fisheries Area. The enlargement shows locations of observation areas A and B, observation towers 1-6, and water-level gauge (g). Arrows on stream indicate direction of water flow.

populations in Pennsylvania, Spruce Creek had the greatest biomass of brown trout: 126 kg/hectare (McFadden and Cooper 1962). The specific conductance is near 285  $\mu$ mhos/cm (McFadden and Cooper 1964; McLaren 1970). Typical values of total nitrate and total phosphorous are 1.6 mg/liter and 0.05 mg/liter, respectively.

The Spruce Creek Experimental Fisheries Area, site of this study, is owned by the Pennsylvania State University and was managed by the Pennsylvania Cooperative Fishery Research Unit for catch and release fly fishing (only) from April 1968 through this study's completion in October 1981. It is located approximately 1 km from the confluence with the Little Juniata River. Within the study area, the stream averages 12.8 m wide, is 1,062 m long, has a 0.8% gradient and a surface area of 1.3 hectares (McLaren 1970) (Fig. 1). The most abundant salmonid in the area is the brown trout (Beyerle and Cooper 1960; McLaren 1970). An electrofishing census (April 28–May 1, 1975) yielded a brown trout standing-crop estimate of 145 kg/hectare. Of 1,427 brown trout captured, less than 5% of the yearling and older fish were over 32 cm total length (Fig. 2). Because young of the year emerge from the gravel in Spruce Creek over an extended period from late March through early May, and are only about 2 cm long when they emerge (Beyerle and Cooper

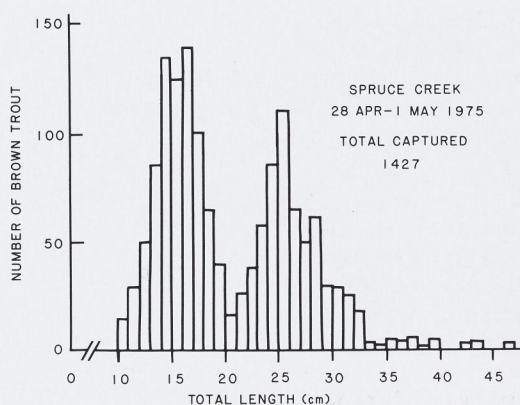


FIGURE 2.—Length frequencies of 1,427 yearling and older brown trout captured by electrofishing in the Spruce Creek Experimental Fisheries Area, April 28–May 1, 1975. The first peak is composed of age group I, second peak, age groups II and older.

1960), they were poorly represented in the census techniques employed, and not included in the 1975 census figures.

The brown trout in the Experimental Fisheries Area are almost exclusively of wild origin. The stream is not stocked by the Pennsylvania Fish Commission except for a short stretch approximately 14 km upstream of the study area. McLaren introduced hatchery-raised brown trout into the research area in 1969 and again in 1971 for experimental purposes but they survived poorly (McLaren 1970, 1979). Private landowners and fishing clubs along the stream stock some brown trout but no trout of recent hatchery origin were found in the 1975 census. These would have been recognized by their comparatively pale coloration and abraded fins.

Other salmonids are rare in the area. Only 17 rainbow trout *Salmo gairdneri* and 3 brook trout *Salvelinus fontinalis* were captured in the 1975 census. Other fish species in the area include the white sucker *Catostomus commersoni*; the tessellated darter *Etheostoma olmstedii*; the slimy sculpin *Cottus cognatus*; and the cyprinids *Rhinichthys atratulus*, *Rhinichthys cataractae*, *Exoglossum maxillingua*, *Notropis cornutus*, and *Pimephales notatus* (Beyerle and Cooper 1960).

The largest pool in the Experimental Fisheries Area is located near the upstream end where the stream splits into three channels (Fig. 1). This pool contained an estimated population of 200 yearling and older wild brown trout in





FIGURE 3.—Observation area A (foreground), towers 1 and 2, at left. Tower 4, by observation area B, is upstream and to the right. Natural vegetation and burlap shielded observers.

1975. The pool, 90 m long from riffle to riffle and 15.2 m wide, has a surface area of approximately 0.14 hectares. The mean summer low flow through the pool at water gage height 0.15 m is  $2.8 \text{ m}^3/\text{second}$ . No fishing was permitted in this pool during the period of the study (June 1977 through October 1981).

### Methods

Brown trout were observed from six camouflaged portable aluminum radar towers erected along the large pool in the upstream part of the Experimental Fisheries Area (Fig. 1). Each tower consisted of two sections that raised the height of eye 1.8 m and 3.3 m above water level. Burlap on the towers and natural vegetation broke the silhouette of observers and permitted entry to the towers without disturbance of the fish (Fig. 3). A wooden roof and visor shielded observers and equipment from rain and prevented reflected sunlight from alarming the fish.

During a pilot study in 1977, I discovered that I could identify individual brown trout by their spot patterns and that the location of individuals within the large pool was very predictable from day to day. I also discovered that the "lies" of the fish (later referred to as foraging sites) were so precise and the manner in which different fish used them so similar that they could be used as spatial references for behavioral observations.

I first observed the brown trout from three towers along each side of the pool. After I de-

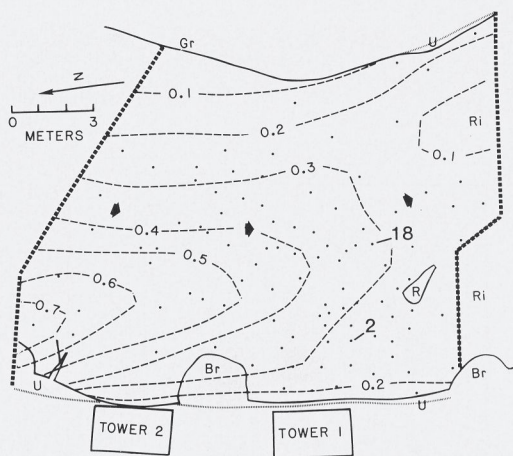


FIGURE 4.—Map of 96 numbered foraging sites in observation area A and mean depth contours in meters. Sites 2 and 18 are labelled. Arrows indicate direction of water flow; R = rock, Br = brush, Gr = gravel bar, U = undercut bank, Ri = riffle.

termined that the behavior of the brown trout was qualitatively the same in all parts of the pool, I selected the tail of the pool (observation area A) for detailed quantitative observation because (1) the surface of the water there was relatively free of ripples, (2) the water shoaled off toward the end of the pool, giving a range of depths in which to observe the fish, and (3) there was less glare and better lighting there. From towers 1 and 2, I also could see some brown trout in riffle habitat (Fig. 4). I constructed a montage of the observation area by fitting together photographs of the bottom. Each foraging site, marked by the location of the eye of the fish occupying it, was assigned a number and located on the montage. The observation area was measured and each foraging site was assigned grid coordinates for subsequent computer analysis.

### Identification of Fish

I identified each brown trout in the observation area by the spot pattern on the left side of the body below the dorsal fin (Figs. 5 and 6). Identification and observation were facilitated by  $7 \times 35$  and  $7 \times 50$  binoculars fitted with polarizing filters.

The fish were photographed from the towers through a 400-mm f/5 telephoto lens fitted with extension tubes to reduce the minimum focus



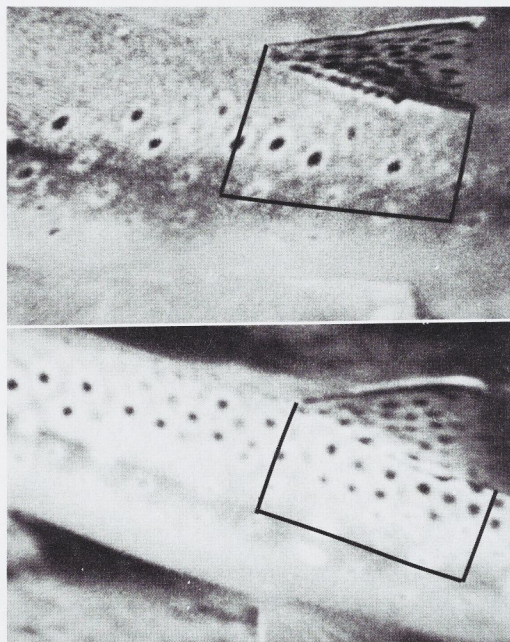


FIGURE 5.—Spot patterns of wild brown trout 31 (top) and wild brown trout 32 (bottom) within rectangular reference areas between the dorsal fin and lateral line.

distance. Kodacolor 35 mm, ASA 400 film gave best resolution, contrast, and color tone. A complete photographic identification file of all fish observed was assembled to ensure positive identification. Wild brown trout were assigned numbers 1 through 79 and hatchery brown trout 80 through 97. Gaps in number series reflect blocks assigned to different observation stations.

#### Observations

Observations were made at all hours of the day from dawn to dusk and in all months of the year for three consecutive years. However, because not all of the observation area could be seen equally well before 0900 or after 1900 hours and because there were very few trout in the main observation area (A) from December through March, only data obtained between 0900 and 1900 hours April through November were included in statistical analyses. Once each hour, each brown trout in the observation area was located and identified ("scan" observations of Altmann 1974). Between these inventories each brown trout was observed in turn for 15 minutes (Altmann's "focal animal" observa-



FIGURE 6.—Identifying spot patterns of 26 wild brown trout whose activity patterns were quantified in this study.

tions). If a particular fish was not in sight when its turn arrived, the next one on the numbered list was observed. By this system, the distribution of brown trout was mapped 10 times a day, and each individual was closely studied (on the average) every 2 days.

Feeding activity was categorized as surface, midwater, and bottom. A feed was recorded if a fish was seen to open its mouth, "chew," or swallow. If a brown trout's head broke the water surface during a feeding excursion, the fish had made a surface feed. If its head touched the bottom, this was a bottom feed. All others were recorded as midwater feeds: that is, the fish fed on organisms suspended in the water column.

The duration and frequency of "false rises," during which a fish rose from its holding position to inspect and reject an item in the drift, were determined from frame-by-frame analysis of videotape recordings.

Agonistic behavior was similar to that described by Kalleberg (1958), Keenleyside and Yamamoto (1962), Jenkins (1969), McLaren



(1979), and North (1979), and as recorded in the Encyclopedia Cinematographica film by Butler and Hawthorne (1975). The start, end, outcome, and location of each agonistic encounter was recorded, together with the identity of the fish involved. The winner was determined by the types of agonistic behavior displayed by each contestant.

Each time a brown trout moved to a different foraging site, the identification number of the site and the time the fish arrived at that site was recorded. Movement rates were later computed by dividing the number of times a fish moved to a new position during an observation period by the total time of the observation period.

The final type of activity recorded was a gape or yawn, characterized by an exaggerated extension of the opercula and upward rotation of the eyes not accompanied by any other movement.

#### *Data Recording*

Recording of observational data was greatly facilitated by the use of a microcomputer system designed specifically for this study. The system consisted of a power supply, KIM-1 programmable microprocessor, clock generator, program memory, random-access memory, and peripheral interface device (MOS Technology 1976). A keyboard allowed manual data input. At the start of each day the computer program was loaded from a cassette tape and the clock was synchronized with real time. Most data entries could be made with one or two keystrokes each because the computer automatically carried a fish's identity and its position in the observation area (entered at the start of each focal animal observation) through subsequent data entries until a new fish code or position code was recorded. Whenever an activity code was entered, the computer automatically recorded the fish's identity, position, and activity, together with date and time to the nearest 0.01 minute. Other codes recorded the start and end of agonistic encounters, the identity of the contestants, and the winner of each bout. Data were dumped to a cassette tape each evening. Later, the data were transferred for editing and processing to the Digital Equipment Corporation Model DEC-10 computer, operated by the Electrical Engineering Department of The Pennsylvania State University.

The activity of fish also was recorded at selected times on 16-mm motion-picture film and on videotape.

#### *Age and Length Determinations*

The age of young-of-the-year and yearling brown trout in Spruce Creek can readily be determined by size alone. The data of Beyerle and Cooper (1960) show no overlap in size between these two age groups in Spruce Creek and also show that most wild brown trout reach 200 mm total length by the end of their second year of growth (see also Fig. 2). Because young of the year in Spruce Creek emerge from the gravel over an extended period from late March through early May (Beyerle and Cooper 1960), March 1 was arbitrarily assigned the "birthday" of all wild fish.

New fish each year consisted of young of the year or yearlings only and many individuals were present throughout the course of the study. Consequently, the exact year class of most of the fish was known by the end of the study. The age of fish larger than 200 mm at the beginning of the study was conservatively estimated to be the minimum age at which fish of known age attained such length. The age of the largest fish, number 15, estimated at 6 in 1979 and 7 in 1980, was later confirmed by examination of the fish's otoliths (sagittae).

The length of individual fish (precision,  $\pm 5$  mm) was determined from photographs taken at known foraging sites. At the end of each season, after brown trout had left for spawning sites, photographs were taken of a metal rule in the exact position previously occupied by the fish. This technique eliminated all effects of parallax and refraction.

#### *Abiotic Variables*

Water temperature, turbidity, water-gage height, and light intensity were recorded for analysis of effect on brown trout behavior (Table 1). Water temperature was recorded continuously with Ryan recording thermographs. Turbidity, in standard nephelometric turbidity units, was measured daily with a Hach turbidimeter. Water height was measured daily with a stream gage installed throughout the duration of the study (Fig. 4). A measure of daily light intensity in arbitrary units was calculated from



the area under the curve of a Belfort recording pyrheliometer.

#### *Hatchery Brown Trout*

On August 23, 1979, after the behavior of the resident population had been studied for approximately 2 years, 200 brown trout were obtained from the Big Spring hatchery in Cumberland County, Pennsylvania, and released in the study area. The hatchery fish were in their second year of growth and ranged from 28 to 35 cm in total length. The left pelvic fin was removed from each before release. They were observed as wild trout had been and those that took up residence were identified by spot patterns. For the first 4 days after the hatchery brown trout were stocked, the activities of both hatchery and wild fish were recorded simultaneously by two observers, who alternated observations between hatchery and wild fish.

To test for a difference in effect of stocking in spring versus late summer, 200 hatchery brown trout again were introduced on May 8, 1980. These, too, were obtained from the Big Spring hatchery and had the left pelvic fin removed, but they were smaller (23–30 cm) than those released the year before.

#### *Analysis*

##### *Statistical Analysis*

All statistical analyses were performed with Statistical Analysis System (SAS) computer programs (SAS Institute 1979).

Regression analyses of length and age were performed on data obtained from 218 photographs of 26 wild brown trout ranging from young of the year to age 8. Because some effect of repeated measures was unavoidable by this technique, confidence intervals reported may be underestimated. Rectangular-hyperbola and negative-exponential models were fitted by the Marquardt iterative method (Marquardt 1963).

Multiple-regression techniques were used to investigate various biotic and abiotic effects on seven behavioral rates: surface, midwater, bottom, and total feeding; agonistic interaction; gape; and movement. Abiotic variables included daily amount of solar incident radiation, water temperature, water turbidity, water height, and temporal effects. Temporal effects were broken down by year, month, and hour of day. Biotic

TABLE 1.—Range and means of abiotic variables for Spruce Creek used in analysis of variance of brown trout activity rates.

Variable	High	Low	Mean $\pm$ SD
Water temperature (C)	20.0	3.1	15.3 $\pm$ 2.5
Turbidity (nephelometric units)	7.5	2.5	4.2 $\pm$ 1.6
Water height (m)	0.22	0.15	0.19 $\pm$ 0.02
Light intensity (arbitrary units)	43 <sup>a</sup>	2 <sup>b</sup>	15.1 $\pm$ 9.4

<sup>a</sup> Cloudless day, midsummer.

<sup>b</sup> Rainy day, late fall.

effects considered were age, length, and dominance ranking of individual fish.

Exploratory analyses techniques revealed that season (month) was the most significant temporal variable and that the effect of year and hour could be ignored in subsequent analyses of variance.

Because the month effect was highly significant, but the interactions of month and the variables of interest were not, month was treated as an indicator variable (Neter and Wasserman 1974) in the formal testing of the effects of the independent biotic and abiotic variables. Any data transformations required to achieve normality are reported in context.

Not all individual fish were equally represented in the observation routine. The identity of all wild fish used in the analyses was known, so the most conservative inferences about the wild population were made by treating all wild individuals with equal weight, even though the total observation time differed from fish to fish. Activity rates were computed for each individual over the time period in question and each such rate was treated as a single datum.

#### *Time Budgets and Bioenergetic Costs*

The time it took wild brown trout to intercept food and to return to the site was determined by frame-by-frame analyses of videotape recordings with a videotape editor. Durations of gapes, agonistic encounters, and position changes were estimated by analysis of videotapes and cinematography. Relative bioenergetic costs of different activity states were estimated from tail-beat frequencies, determined similarly by analysis of videotapes and motion-picture sequences. The effect of fish size on tail-



TABLE 2.—Observations of brown trout in Spruce Creek: number of scans (quick inventories) during which a fish was sighted, and number of minutes a fish was observed during 15-minute studies of them (focal observations), 1978–1980.

Fish number	1978				1979				1980			
	Age	Rank	Focal minutes observed	Number of scans	Age	Rank	Focal minutes observed	Number of scans	Age	Rank	Focal minutes observed	Number of scans
1	3	5	354	44								
3					1	7	102	118	2	12	45	115
5	3	6	485	88	4	6	322	263				
7	4	1	350	63	5	5	221	105				
8	1	14	1,092	146	2	12	604	332	3	10	418	193
10	2	4	191	74	3	4	139	75	4	14	61	26
11	1	14	38	17	2	11	216	264	3	11	183	150
14	3	3	18	4	4	3	149	109	5	3	49	55
15	5	1	16	6	6	1	173	75	7	1	102	118
22	1	13	157	96								
23	2	12	431	111	3	8	205	198				
24	3	10	204	103	4	12	168	165				
30									1	15	102	108
31	2	9	1,501	145	3	9	466	254	4	9	576	184
32	2	11	1,041	131	3	11	554	310	4	11	166	69
34	2	13	747	128	3	10	414	301				
36									1	14	156	116
37									1	15	64	31
44	2	10	92	11	3	10	13		4		14	28
45	2	12	99	13								
51	4	2	51	9	5	2	126	145	6			
52	1	15	16	32	2	13	198	258				
53					1	14	289	231	2	14	205	166
54					1	15	125	121	2	13	124	109
57					1	13	131	114	2	12	181	153
62					1	13	109	75				
Hatchery					1		558		1		1,174	

beat frequency was small compared to the effects of activity states and was ignored.

#### Home Range

Home-range size was estimated from the areas of both the minimum convex polygon that enclosed 95% of the sightings of each fish (A1 index) and an ellipse based on the determinant of the covariance matrix of the sightings (A4 index of Jennrich and Turner 1969). The latter index is a parametric estimate of the area that accounts for 95% of the habitat used by each wild brown trout.

The utilization distribution (Jennrich and Turner 1969; Anderson 1982) of each wild brown trout, a nonparametric estimate of home range, was generated by a computer-mapping program called SYMAP (Dougenik and Sheehan 1975). This program creates a contour map by interpolating a continuous surface in the region where there are no data points. A three-

dimensional visual representation of the utilization distribution was created by a computer-graphics program SYMVU (LCGSA 1977).

#### Behavior of Wild and Hatchery Fish

Because not all hatchery brown trout had been individually identified at the start of the comparative study, activities were analyzed on the basis of observation periods rather than individual fish. This resulted in a certain amount of repeated measures, but was unavoidable. Consequently, confidence intervals reported for comparative behavior of hatchery and wild trout may be underestimated.

The data were partitioned into two separate distributions for analysis: (1) rates, given that the activity did occur during an observation (zero rates were dropped from the analyses); and (2) proportions of observations in which an activity did or did not occur. The former distributions then were tested for normality; if an appropri-



ate transformation achieved normality, a *t*-statistic was calculated to test the hypothesis that the means of two groups of data are unequal.

The difference in proportions of non-zero observations between hatchery and wild activity was tested with the  $(1 - \alpha)$  confidence interval for the difference between the proportions of a binomial distribution (Walpole and Myers 1972;  $\alpha$  is the probability of a type-I error, and  $[1 - \alpha]$  is converted to percent).

### Results

Of the 18 wild brown trout resident in observation area A in 1978, 15 were present again in 1979. Twelve of the 20 fish observed in 1979 returned again in 1980 (Table 2). Both in 1979 and 1980, all new fish were young of the year or yearlings. Even though it was suspected that two or three older fish were removed by poachers early in the spring of 1980 (fish 51 had been positively identified in March) no age-group 2 or older brown trout moved in to take their places.

#### Home Range

The mean home-range size of 53 wild brown trout was 15.6 m<sup>2</sup> (SE, 1.7) as determined from minimum-convex polygons encompassing 95% of the scan sightings of each fish each year. The home-range size decreased steadily during the second through fifth years of growth (age groups 1–4) (Spearman's rank correlation coefficient  $r = -0.34$ ;  $P = 0.02$ ;  $N = 47$ ) but then increased (Fig. 7). Home-range estimates based on the bivariate normal assumptions of Jennrich and Turner (1969) also yielded a negative but nonsignificant correlation (Spearman's  $r = -0.15$ ;  $P = 0.31$ ) for age groups 1–4, and an overall mean area of 47.7 m<sup>2</sup>, three times that obtained by the polygon technique.

Each wild brown trout used only a portion of the total 182-m<sup>2</sup> observation area and remained faithful to the same part of the area from year to year (Fig. 8). No fish had exclusive use of any home range; considerable overlap existed in the home ranges of neighboring wild brown trout. For example, in 1979 the home range of fish 31 was wholly contained within that of fish 10, site 18 being the most frequently used foraging site by both fish (Fig. 9). None of the 20 wild brown trout resident in area A in 1979 was ever seen in area B despite over 100 hours of obser-

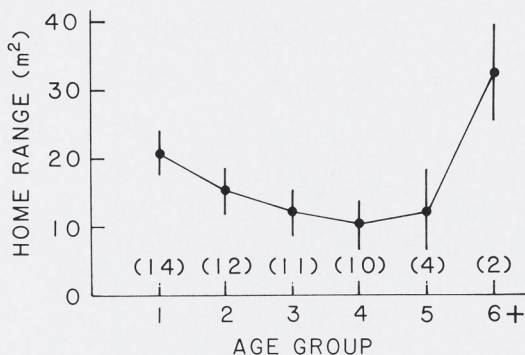


FIGURE 7.—Mean size ( $\pm$ SE) of home ranges for six age groups of wild brown trout as determined by the minimum-convex-polygon method. Sample sizes are in parentheses.

vation from tower 4. Neither was any of the eight brown trout resident in area B ever seen in area A, although area B was less than 30 m upstream and in the same pool as area A (Figs. 2 and 3). This is further confirmation of the small home ranges used by wild brown trout in Spruce Creek.

#### Foraging and Refuge Sites

Within their home range, individual wild brown trout used from 1 to 32 foraging sites, the mean number accounting for 90% of focal animal observations being  $6.0 \pm 0.5$  (SE;  $N = 52$  fish). From these sites, the fish darted to intercept food items in the drift and to pick up organisms attached to or moving about on the substrate.

Typically, foraging sites were in front of a submerged rock, or on top of but on the downward-sloping rear surface of a rock (Fig. 10). From there the fish had an unobstructed view of oncoming drift. While a wild brown trout was in such a site, its tail beat was minimal (see page 23), indicating that little effort was required to maintain a stationary position even though the current only millimeters overhead was as high as 60 to 70 cm/second. Most brown trout could be found in one of several such sites day after day (Fig. 10), and it was not uncommon to find a fish using many of the same sites for three consecutive years (Fig. 11).

The precision with which brown trout used foraging sites gives an indication of the latter's function and importance. The position of the



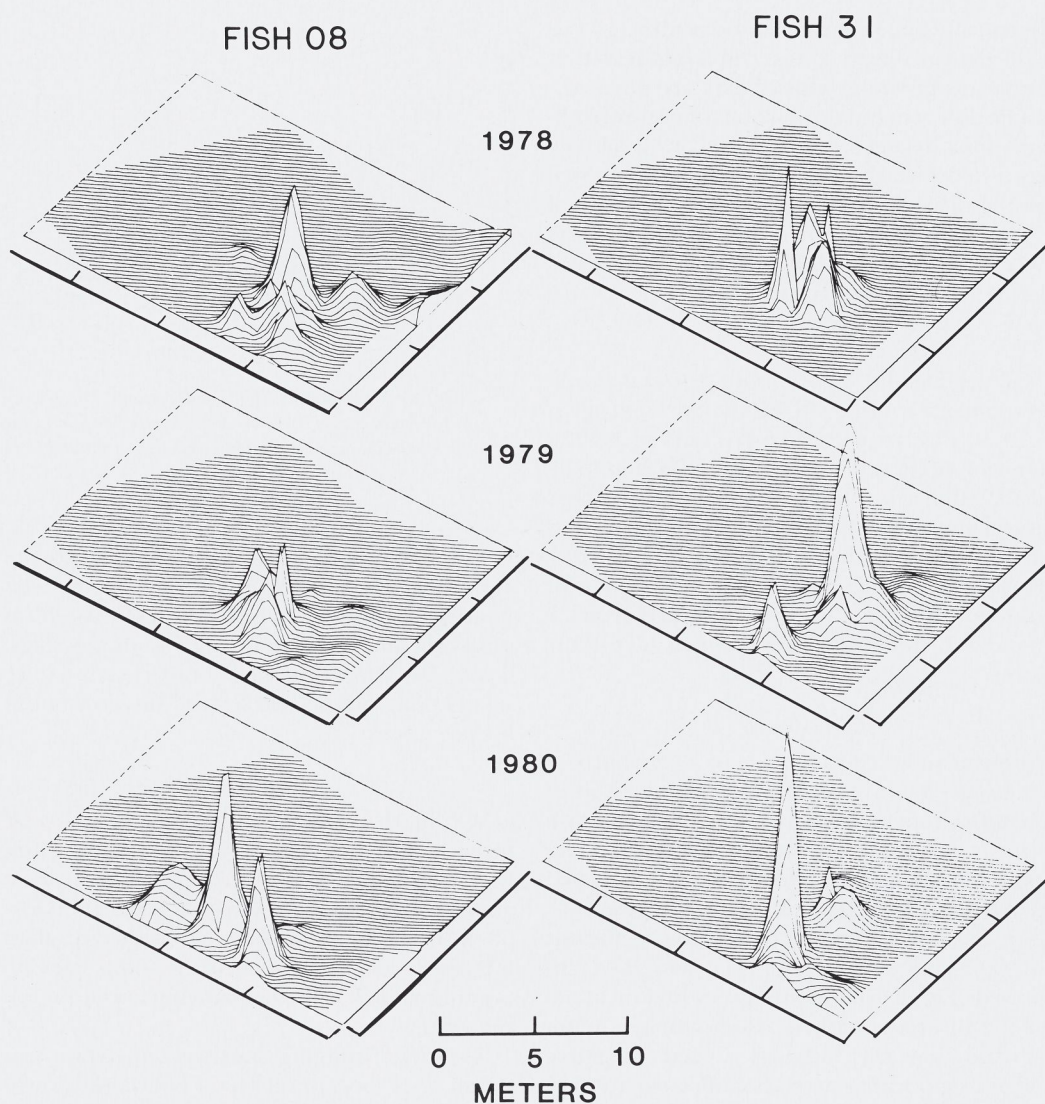


FIGURE 8.—Utilization distributions for wild brown trout 8 (year class 1977) and wild brown trout 31 (year class 1976) in 1978, 1979, and 1980. Shaded area represents observation area A. Peaks represent percent of time the fish was observed in specific foraging sites.

eye of fish 31 in position 18 (Fig. 10) in eleven photographs taken over 15 months ranged less than 40 mm in a longitudinal stream direction (SD, 11.7 mm), and cross-stream range was less than half of that. The position of the eye of fish 32 in the three photographs of Fig. 11 is virtually identical. This precision, together with the ease with which the wild brown trout were able to maintain these positions, demonstrates the cost-minimizing utility of the sites.

Many sites were used by more than one brown trout during a day (Fig. 9). Different fish used a particular site in the same way and with the same precision. Even though some smaller rocks shifted and moved during the course of the study, the foraging sites, created by the unique flow of water over and around the larger embedded rock, remained fixed. The most distinctive characteristic of the foraging sites was the low water velocity (about 8 cm/second) in



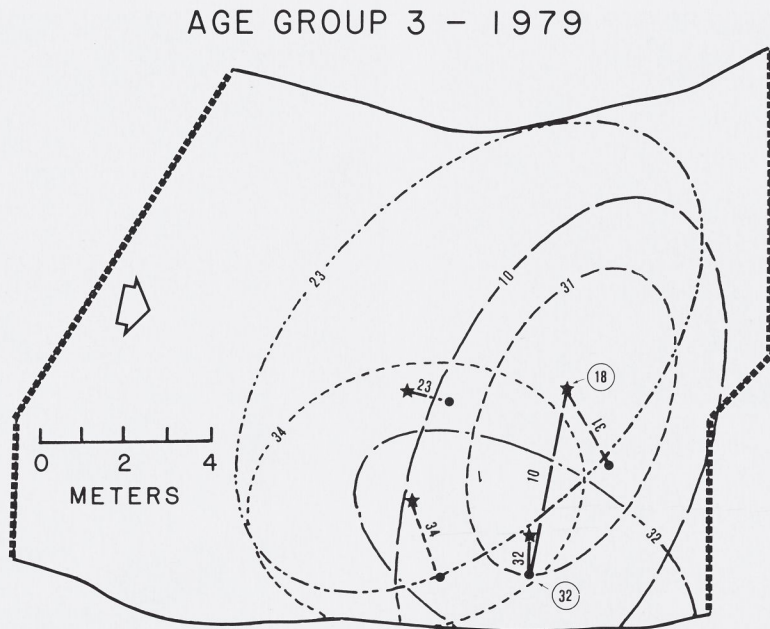


FIGURE 9.—Home ranges of five age-3 wild brown trout in 1979, as estimated by the Jennrich and Turner (1969) method. Site 18 was the primary (most often used) site for both fishes 10 and 31 and site 32 was the secondary site for both fishes 10 and 32 that year. Primary sites are indicated by stars, secondary sites by dots.

the immediate vicinity of the resident brown trout's head (Pierce 1982).

The precision with which brown trout used foraging sites precluded there being more than one fish at a site at a time. The distance between adjacent occupied foraging sites was rarely less than 1.5 m and if two brown trout were feeding within sight of each other, the larger of the two was always upstream.

Refuge sites were those sites to which trout fled when disturbed. Because wild brown trout rarely used refuge sites and because the experimental design of the study precluded observation of some fish in refuge sites, comments concerning these sites must be considered anecdotal.

The overhead flight of a large bird such as a mallard *Anas platyrhynchos* or common grackle *Quiscalus quiscula* typically caused a wild brown trout to dart to one side or another and become motionless with its body pressed tightly to the substrate. With no further stimulus, the fish would usually return to its foraging site and resume feeding within 3 to 5 minutes. Repeated alarm stimulus or stronger initial stimulus (such as a mallard landing) would cause the fish to

flee to deep water and become motionless or to move under a bank, rock, or some brush. In such a case, the fish would usually return to a foraging site in about 20 to 30 minutes.

Typically, more than one wild brown trout fled to the same pocket of deep water or under the same bank, rock, or brush. On one occasion a 2-year-old brown trout was observed tucked tightly along and partly under the down-stream side of a flat rock, perpendicular to the flow of the stream. It remained there for about 2 hours without any movement. It suddenly left this position, proceeded to one of its accustomed foraging sites, and started feeding. Other brown trout were occasionally seen lying motionless under brush (sometimes only the tip of the tail could be seen). Fish in refuge sites did not feed, did not move, and engaged in no agonistic encounters.

#### *Feeding, Position Change, and Gaping*

The mean total feeding rate, averaged over all months from April through November, steadily declined with increasing age from 20.2 feeds per 15 minutes for age-group 1 to 5.6 feeds per 15 minutes for age-group 6+ (Fig. 12;





FIGURE 10.—Wild brown trout 31 in site 18 on successive days during summer 1979.

Tables 3 and 4). The proportion of surface and midwater feeds was approximately the same for all age groups; bottom feeds accounted for only 7–13% of the total. On numerous occasions, small fish fed close to, but downstream from, a larger, more dominant fish, and at a higher rate than the upstream dominant. The larger fish

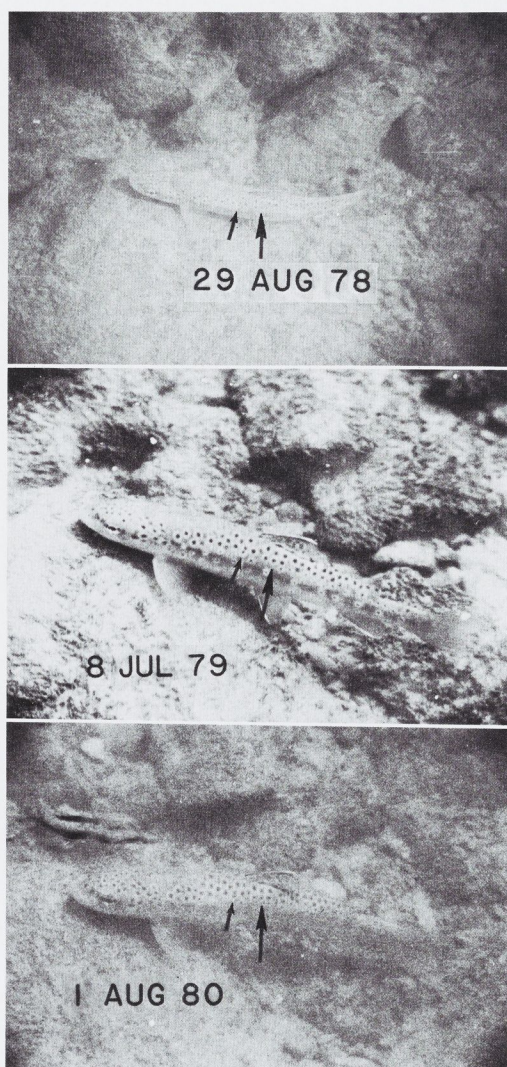


FIGURE 11.—Wild brown trout 32 in site 2 in three successive summers. The rectangular group of six spots below the dorsal fin (large arrow) and the two small spots close together (small arrow) were key identifying features.

was passing up some items in the drift that the smaller wild brown trout ate.

Feeding rates were highest in spring, declined in July and August, and then increased again in September and October. Surface and midwater rates were about equal April through August but surface feeding was predominant in fall. Mean bottom-feeding rate was low throughout the year (Table 3).

Total feeding rates were higher on days when



older fish were seen in observation area A. The mean feeding rate (feeds per 15 minutes) of young fish (age groups 1–4) on days when age groups 5 and older were seen in daily scan observations was  $20.4 \pm 2.1$  (SE;  $N = 49$ ), and it was only  $15.4 \pm 0.8$  ( $N = 67$ ) when older fish were not seen ( $F = 6.40$ ;  $P = 0.013$ ).

Total and midwater feeding rates were significantly higher on sunny days than on cloudy days. Increase in water temperature appeared to have a depressing effect on midwater and total feeding rates, even when corrected for the effect of month (Table 4). The only significant effect of turbidity was a depressing effect on bottom-feeding rates.

The number of times a fish moved from one foraging site to another during a 15-minute observation was highest in April and May and declined steadily throughout the rest of the year (Table 3). Neither size nor age had a significant effect on movement rate of the younger fish (<4 years old) but larger fish (older than age 3) moved less than younger fish (Tables 3 and 4). The time of day had no significant effect on the movement rates of the fish (Table 3), nor did any of the abiotic variables measured: turbidity; light intensity; water temperature; water height (Table 4).

There was a very pronounced temporal effect on the rate at which the fish gaped, which was highest during summer months and lowest during the middle of the day (Fig. 13). When corrected for the confounding effect of month, gape rate was highly correlated with water temperature, but turbidity had no significant effect (Table 4). No difference in the frequency of gaping was evident among the various age groups.

#### Growth

Growth of brown trout was curvilinear with age; a rectangular hyperbola fit the data better than a negative exponential, which gave too low an asymptotic length (Table 5, Fig. 14). For the rectangular hyperbola, parameter estimates did not differ between the model of all fish and of the subset of fish aged 0–4 (regression analysis;  $P \leq 0.05$ ), indicating that the lengths of older fish could be predicted by the growth of younger age groups.

Growth of older brown trout in the study area was very slow. This is exemplified by fish 15, dominant in the area during 1978, 1979, and

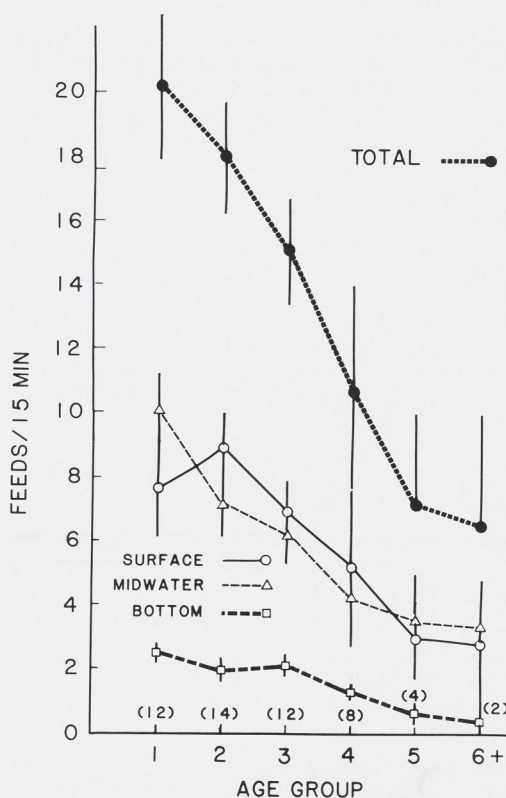


FIGURE 12.—Mean ( $\pm$ SE) feeding rates for six age groups of wild brown trout: total rates and rates for surface, midwater, and bottom feeding. Number of fish in each age group is in parentheses.

1980. In August 1977, it was 28.3 cm long and it grew slightly less than 4 cm over the next 4 years. Scale samples taken from this fish in October 1981 yielded only one unregenerated scale out of 78 taken, and that scale contained only three distinct annuli. Fish 15 was captured and killed in April 1982. The otoliths (sagittae) displayed 9 distinct annuli, confirming the age estimates used for this fish throughout the study.

#### Dominance Hierarchy

Dominance hierarchies of wild brown trout in observations area A were nearly linear and quite consistent from year to year (Fig. 15, Tables 6–8). Fish 15, never observed to lose an agonistic encounter in 3 years, ranked first. Other wild brown trout were ranked 2–15, based on the number of fish in the longest linear chain, which occurred in 1979. Dominance was strongly correlated with age (Spearman's  $r =$



TABLE 3.—Activities of wild brown trout in observation area A of Spruce Creek, stratified by age group, time of day, and season. Within a stratum, means with a letter in common are not significantly different (Duncan's multiple-range test;  $P > 0.05$ ).

Age, hour or month	Number of fish	Mean number per 15 minutes $\pm$ SE							Number of focal observations	
		Agonistic encounters	Feeds					Gapes		
			Surface	Midwater	Bottom	Total	Moves			
Age										
1	12	2.1 $\pm$ 0.5 a	7.6 $\pm$ 1.6 ab	10.0 $\pm$ 1.2 a	2.6 $\pm$ 0.3 a	20.2 $\pm$ 2.2 a	2.6 $\pm$ 0.6 a	1.08 $\pm$ 0.16 a	168	
2	14	1.8 $\pm$ 0.2 a	8.9 $\pm$ 1.0 a	7.1 $\pm$ 1.0 ab	1.9 $\pm$ 0.2 ab	18.0 $\pm$ 1.7 a	2.5 $\pm$ 0.5 a	0.79 $\pm$ 0.10 a	350	
3	12	1.9 $\pm$ 0.3 a	6.9 $\pm$ 1.0 ab	6.1 $\pm$ 0.8 b	2.1 $\pm$ 0.4 ab	15.1 $\pm$ 1.7 ab	2.9 $\pm$ 0.7 a	0.75 $\pm$ 0.15 a	252	
4	8	1.7 $\pm$ 0.2 a	5.2 $\pm$ 2.5 ab	4.2 $\pm$ 1.0 b	1.3 $\pm$ 0.2 bc	10.8 $\pm$ 3.2 ab	1.2 $\pm$ 0.6 a	0.85 $\pm$ 0.14 a	133	
5	4	2.0 $\pm$ 0.2 a	2.9 $\pm$ 1.2 b	3.5 $\pm$ 1.4 b	0.6 $\pm$ 0.2 cd	7.1 $\pm$ 2.8 b	2.7 $\pm$ 0.4 a	0.86 $\pm$ 0.40 a	38	
6+	2	0.8 $\pm$ 0.1 b	2.8 $\pm$ 2.6 ab	3.3 $\pm$ 1.3 b	0.4 $\pm$ 0.1 cd	6.6 $\pm$ 3.6 b	1.1 $\pm$ 0.6 a	0.34 $\pm$ 0.31 a	21	
Hour of the day <sup>a</sup>										
0900	27	0.9 $\pm$ 0.2	6.7 $\pm$ 1.7	5.3 $\pm$ 0.9	1.9 $\pm$ 0.4	13.8 $\pm$ 2.2	2.0 $\pm$ 0.3	1.05 $\pm$ 0.10	105	
1000	33	1.1 $\pm$ 0.2	5.3 $\pm$ 1.0	5.6 $\pm$ 0.7	2.0 $\pm$ 0.5	12.8 $\pm$ 1.5	2.7 $\pm$ 0.4	1.19 $\pm$ 0.16	105	
1100	30	1.5 $\pm$ 0.3	6.2 $\pm$ 0.9	5.4 $\pm$ 0.7	1.6 $\pm$ 0.3	13.2 $\pm$ 1.4	3.6 $\pm$ 0.5	0.94 $\pm$ 0.10	113	
1200	26	1.0 $\pm$ 0.2	6.3 $\pm$ 1.1	5.7 $\pm$ 0.7	2.2 $\pm$ 0.4	14.3 $\pm$ 1.3	2.7 $\pm$ 0.1	0.70 $\pm$ 0.10	98	
1300	27	1.4 $\pm$ 0.2	5.5 $\pm$ 1.0	6.9 $\pm$ 1.4	1.6 $\pm$ 0.3	13.9 $\pm$ 2.1	3.3 $\pm$ 0.4	0.60 $\pm$ 0.10	135	
1400	30	1.2 $\pm$ 0.2	8.2 $\pm$ 2.4	7.0 $\pm$ 1.1	1.9 $\pm$ 0.4	17.1 $\pm$ 2.5	3.0 $\pm$ 0.5	0.63 $\pm$ 0.08	117	
1500	30	1.4 $\pm$ 0.2	6.3 $\pm$ 1.4	8.1 $\pm$ 1.5	1.9 $\pm$ 0.3	16.3 $\pm$ 2.1	2.9 $\pm$ 0.4	0.95 $\pm$ 0.17	95	
1600	33	1.3 $\pm$ 0.2	4.2 $\pm$ 0.8	7.4 $\pm$ 1.8	1.3 $\pm$ 0.3	12.9 $\pm$ 2.6	2.4 $\pm$ 0.4	1.00 $\pm$ 0.12	104	
1700	22	1.1 $\pm$ 0.2	7.2 $\pm$ 1.8	6.3 $\pm$ 1.3	1.8 $\pm$ 0.4	15.3 $\pm$ 2.6	1.7 $\pm$ 0.3	0.96 $\pm$ 0.12	61	
1800	10	1.0 $\pm$ 0.5	5.3 $\pm$ 1.4	6.1 $\pm$ 1.5	1.3 $\pm$ 0.5	12.7 $\pm$ 2.7	1.8 $\pm$ 0.5	0.97 $\pm$ 0.23	14	
Month										
Apr	9	0.9 $\pm$ 0.3 cd	8.6 $\pm$ 2.4 ab	8.6 $\pm$ 1.7 a	6.0 $\pm$ 2.3 a	23.2 $\pm$ 3.0 a	4.4 $\pm$ 1.6 ab	0.04 $\pm$ 0.04 d	21	
May	22	1.7 $\pm$ 0.4 ab	8.3 $\pm$ 1.8 a	9.9 $\pm$ 0.7 a	2.9 $\pm$ 0.6 a	21.1 $\pm$ 2.0 a	4.3 $\pm$ 0.5 a	0.72 $\pm$ 0.11 ab	125	
Jun	20	1.9 $\pm$ 0.3 a	9.6 $\pm$ 2.1 a	10.9 $\pm$ 2.5 a	2.5 $\pm$ 0.7 a	23.0 $\pm$ 3.7 a	3.6 $\pm$ 0.3 ab	0.90 $\pm$ 0.12 ab	166	
Jul	27	0.9 $\pm$ 0.1 bc	7.2 $\pm$ 1.0 ab	7.9 $\pm$ 1.1 a	1.7 $\pm$ 0.2 a	16.8 $\pm$ 1.7 ab	2.8 $\pm$ 0.2 b	1.07 $\pm$ 0.15 a	261	
Aug	30	1.0 $\pm$ 0.2 cd	3.8 $\pm$ 0.7 bc	3.7 $\pm$ 0.6 b	1.6 $\pm$ 0.2 a	9.1 $\pm$ 1.2 d	2.1 $\pm$ 0.2 bc	0.87 $\pm$ 0.13 a	329	
Sep	12	1.2 $\pm$ 0.7 cd	9.2 $\pm$ 2.5 ab	2.8 $\pm$ 0.6 b	0.5 $\pm$ 0.2 b	12.5 $\pm$ 2.7 cd	1.3 $\pm$ 0.4 cd	0.54 $\pm$ 0.24 bc	30	
Oct	10	0.7 $\pm$ 0.2 cd	12.1 $\pm$ 3.2 a	2.6 $\pm$ 0.3 b	0.7 $\pm$ 0.2 b	15.4 $\pm$ 3.4 bc	1.0 $\pm$ 0.4 cd	0.07 $\pm$ 0.05 d	20	
Nov	7	0.3 $\pm$ 0.2 d	1.1 $\pm$ 0.4 c	0.5 $\pm$ 0.2 c	0.7 $\pm$ 0.2 b	2.3 $\pm$ 0.8 e	0.8 $\pm$ 0.3 cd	0.16 $\pm$ 0.08 cd	22	

<sup>a</sup> No significant effect of time of day on any activity.

0.81;  $P = 0.01$ ;  $N = 50$ ), although the agonistic encounter rate was essentially the same for age groups 1 through 5 (Table 3). There was no significant effect of dominance on any of the seven behaviors tested (Table 4). Agonistic encounter rates were highest in May and June, corresponding to the months of highest feeding rates (Table 3), but time of day had no significant effect on agonistic behavior. Of the four abiotic variables measured, only water height had a significant (positive) effect on agonistic behavior (Table 4).

#### Use of Cover

One of the most surprising results of this study was the high probability of sighting an individual wild brown trout in a foraging site during scan and focal-animal observations. Age-2 wild brown trout were found during 83% of the scans between 0900 and 1900 hours. If one defines

"cover" as concealment from above, age-2 brown trout spent less than 17% of those hours under cover. As the fish got older, they were less likely to be seen (Fig. 16). Because part of the home range of some fish was not wholly within the observation area and the cryptic coloration of the fish inevitably results in some fish being missed in a scan observation, the data in Fig. 16 must be considered very conservative estimates of the time the fish were not under overhead cover. The overall mean probability of sighting an individual of any age group (given that it was seen at least once that day) ranged from a low of  $0.64 \pm 0.07$  (SE) in April and May to  $0.81 \pm 0.02$  in November.

#### Time and Energy Budgets

It took brown trout only 1 second to intercept food items in the drift or capture organisms on the bottom from their stationary foraging sites,



TABLE 4.—Relationships of activity rates (events / 15 minutes) of wild brown trout in Spruce Creek with fish age, length, dominance rank, and abiotic variables, corrected for effect of month. Asterisks (\*) indicate significant slopes ( $P \leq 0.05$ ). Abbreviations:  $b$  = slope;  $P$  = probability;  $N$  = number of observations; Trans = transformation of dependent variable (CBRT = cube root;  $1/X$  = inverse of dependent variable; SQRT = square root).

Independent variable	Agonistic encounters	Feeds				Gapes	Moves
		Surface	Midwater	Bottom	Total		
Age							
<i>b</i>	−0.0009	−0.0275*	−0.0219*	+0.0048*	−0.1787*	+0.0006	−0.0100*
<i>P</i>	0.3766	0.0003	0.0001	0.0001	0.0001	0.4510	0.0006
<i>N</i>	137	170	152	152	183	132	152
Trans	1/ <i>X</i>	CBRT	Log <sub><i>e</i></sub>	1/ <i>X</i>	SQRT	1/ <i>X</i>	Log <sub><i>e</i></sub>
Length							
<i>b</i>	−0.0044	−0.0366*	−0.0640*	+0.0125*	−0.1415*	+0.0016	−0.0278*
<i>P</i>	0.2272	0.0005	0.0001	0.0001	0.0001	0.5430	0.0051
<i>N</i>	137	171	152	152	185	132	152
Trans	1/ <i>X</i>	CBRT	Log <sub><i>e</i></sub>	1/ <i>X</i>	SQRT	1/ <i>X</i>	Log <sub><i>e</i></sub>
Dominance							
<i>b</i>	−0.0044	−0.0517	+0.0104	−0.0039	−0.0355	+0.0024	+0.0338
<i>P</i>	0.6004	0.0530	0.4926	0.4637	0.4881	0.7007	0.1716
<i>N</i>	48	46	50	50	51	47	50
Trans	1/ <i>X</i>	CBRT	Log <sub><i>e</i></sub>	1/ <i>X</i>	SQRT	1/ <i>X</i>	Log <sub><i>e</i></sub>
Turbidity							
<i>b</i>	−0.0013	−0.0237	−0.0732	+0.0431*	−0.1690	+0.0019	−0.0597
<i>P</i>	0.3114	0.6727	0.1624	0.0002	0.0847	0.8550	0.3244
<i>N</i>	173	153	173	126	186	109	145
Trans	1/ <i>X</i>	Log <sub><i>e</i></sub>	Log <sub><i>e</i></sub>	1/ <i>X</i>	SQRT	1/ <i>X</i>	Log <sub><i>e</i></sub>
Light intensity							
<i>b</i>	−0.0009	+0.0097	+0.0097*	+0.0019	+0.0077*	+0.0003	−0.0015
<i>P</i>	0.4598	0.1119	0.0351	0.0633	0.0374	0.6974	0.8112
<i>N</i>	171	250	279	211	293	175	224
Trans	1/ <i>X</i>	Log <sub><i>e</i></sub>	Log <sub><i>e</i></sub>	1/ <i>X</i>	SQRT	1/ <i>X</i>	Log <sub><i>e</i></sub>
Water temperature							
<i>b</i>	−0.0031	+0.0231	−0.0543*	+0.0083	−0.0642*	−0.0179*	+0.0567
<i>P</i>	0.7279	0.5055	0.0385	0.1775	0.0016	0.0020	0.1607
<i>N</i>	252	371	417	339	401	290	299
Trans	1/ <i>X</i>	Log <sub><i>e</i></sub>	Log <sub><i>e</i></sub>	1/ <i>X</i>	SQRT	1/ <i>X</i>	Log <sub><i>e</i></sub>
Water height							
<i>b</i>	−0.6932*	−1.1846	+1.3345	−0.1789	+3.0000	−0.2479	−0.5911
<i>P</i>	0.0099	0.3056	0.1806	0.4517	0.1112	0.1781	0.5709
<i>N</i>	136	193	217	160	230	135	176
Trans	1/ <i>X</i>	Log <sub><i>e</i></sub>	Log <sub><i>e</i></sub>	1/ <i>X</i>	SQRT	1/ <i>X</i>	Log <sub><i>e</i></sub>

but because the current swept the fish farther downstream during a surface feed it took the fish longer (6 seconds) to return to the site after a surface feed than for either a midwater or bottom feed (Table 9). A rough approximation of the comparative energetic cost of the several activities may be obtained from the tail-beat frequencies of the trout in different activity states (Table 10). The high energetic cost of surface feeding is evident from the relative duration of, and tail-beat frequency during, surface feeding. Stationary swimming at the surface, an even more costly activity, was very rare (much less

than 1% of observations) and always was associated with very high feeding rates (30–40 feeds/15 minutes). The percent of time spent in each behavioral state for each age group was calculated from the general equation:

$$\% \text{ activity} = 100(\text{mean duration of activity} \times \text{mean activity rate}) / \text{observation time}.$$

The wild brown trout in Spruce Creek spent less than 14% of their foraging time in energetically costly activity (Table 11). They spent most of their daylight time, an average of 86%, in a sit-and-wait state, searching the passing



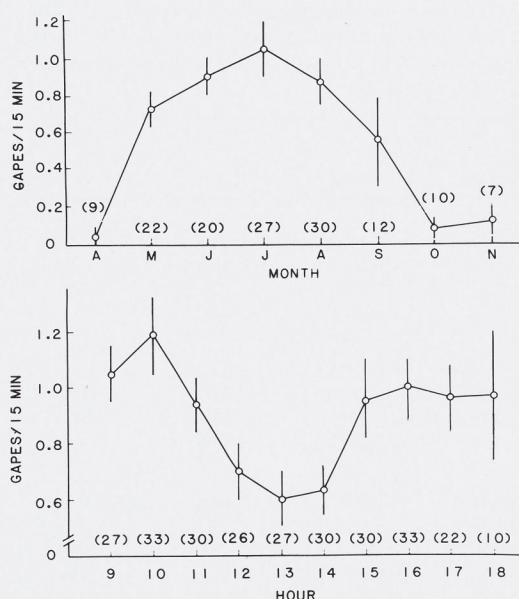


FIGURE 13.—Mean ( $\pm$ SE) gape rates of wild brown trout for April through November and 0900–1900 hours averaged over 3 years (1978–1980). Number of fish is in parentheses.

water column for drifting food. The cost-saving value of such behavior is evident from the low tail-beat frequencies and time spent in such states. As the fish got older, a greater proportion of time was spent in agonistic encounters and a smaller proportion in pursuit of food. Overall, the fish became less active as they got older (Table 11).

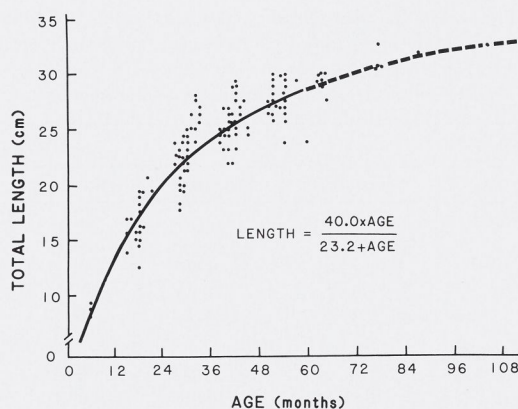


FIGURE 14.—Length-age relationship for wild brown trout in Spruce Creek. Dots are empirical; the rectangular hyperbola was fitted to them by least-squares. Broken portion of curve reflects minimum age estimates of trout older than 4+.

#### Hatchery Brown Trout

Within 20 minutes after the hatchery fish were introduced, the wild brown trout engaged the hatchery fish in agonistic encounters. Most agons were started by the wild fish but there was no prior residence effect in the outcome of encounters between wild and hatchery fish. Of 197 contests, 83 were won by wild fish and 96 were won by hatchery fish (Tables 7 and 8). There was, however, a significant correlation between the dominance rank of the wild fish (as determined from agonistic encounters among wild fish) and the proportion of agonistic encounters between wild and hatchery fish that a

TABLE 5.—Growth models for brown trout in Spruce Creek, fit by nonlinear regression.  $L_{max}$  and  $L_0$  are asymptotic total lengths for rectangular-hyperbola and exponential models, respectively.  $A_{1/2}$  is age at which half of asymptotic length is attained;  $B_1$  is exponential time constant.

Model	N	Sum of squares	Parameter		
			Symbol	Estimate	Asymptotic 95% confidence interval
Rectangular hyperbola <sup>a</sup>	218	Regression, 128,333.6	$L_{max}$	40.0 cm	38.4, 41.6
		Residual, 643.8	$A_{1/2}$	23.2 months	20.7, 25.7
Rectangular hyperbola <sup>a</sup> (ages 0–4 only)	154	Regression, 76,897.6	$L_{max}$	40.3 cm	37.0, 43.6
		Residual, 539.3	$A_{1/2}$	23.6 months	19.1, 28.0
Negative exponential <sup>b</sup>	218	Regression, 128,316.9	$L_0$	30.8 cm	30.0, 31.6
		Residual, 660.4	$B_1$	0.045	0.041, 0.047

<sup>a</sup> Rectangular hyperbola model:  $L = L_{max}Age / (A_{1/2} + Age)$ .

<sup>b</sup> Negative exponential model:  $L = L_0[1 - \exp(-B_1Age)]$ .



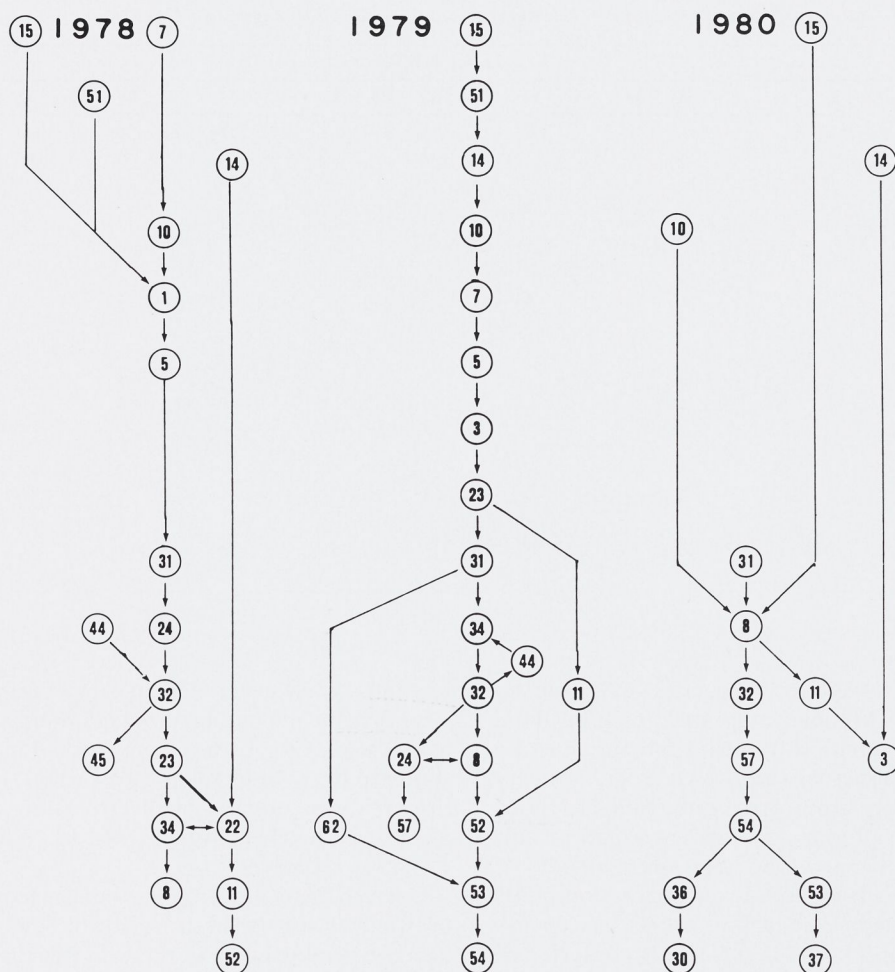


FIGURE 15.—Social hierarchies of wild brown trout resident in observation area A, 1978–1980, based on outcomes of agonistic encounters. Highest rank is at top. Number in circle is the fish identification number.

wild fish won ( $r = -0.37$ ;  $P = 0.03$ ;  $N = 32$ , Spearman's rank correlation coefficient). The large, high-ranking wild fish repeatedly chased the hatchery fish completely out of the observation area. Fish 15, the oldest wild brown trout in observation area A, never lost an agonistic encounter with any brown trout, wild or hatchery, during the observation periods 1978 through 1980 (Tables 6–8). Although agonistic encounters between wild brown trout rarely exceeded 30 seconds, those between wild and hatchery trout were frequently very prolonged. On one occasion wild fish 31 engaged seven hatchery fish in a series of agonistic bouts that

lasted 3.5 minutes. At the end of this series, fish 31 was breathing heavily, had a dark, blotchy color, and appeared exhausted. Other wild brown trout similarly exhibited evidence of stress, not seen before the introduction of hatchery fish.

A few hatchery brown trout took up stationary positions in foraging sites used by wild brown trout. Some hatchery trout were observed in these discrete sites only minutes after they were stocked and before they had started to feed. They used these common sites with a precision similar to that of the wild brown trout. A few hatchery brown trout displaced wild fish from



TABLE 6.—Outcomes of agonistic encounters between brown trout (identified by number), 1978.

Winning fish	Losing fish																		Total wins
	1	5	7	8	10	11	14	15	22	23	24	31	32	34	44	45	51	52	
1	—	2								1		1	2	2	2	1			11
5		—		2	1					1		8	4	3		2			21
7	2	3	—	4	3					1	4	3	1	5					26
8	1			—										2					3
10	1			3	—	4				1		10	4	1				3	27
11						—													0
14							—		3									1	4
15	1							—						1					2
22						1			—			1		1					3
23				2		1			1	—				4					8
24										1	—		2						3
31		3		46	3				8	7	1	—	16	11		1		3	99
32		1		19	1					1		2	—	7	1	8			40
34				5					1	1	1			—					8
44				2										6		1			9
45																—			0
51	1									1				1			—	1	4
52																		—	0
Total losses	5	10	0	83	8	6	0	0	13	15	6	25	35	38	3	13	0	8	268

these preferred foraging sites and even appeared to become integrated into the dominance hierarchy of the wild fish for short periods. Unlike the wild brown trout, however, the hatchery brown trout often failed to return to the site after an agonistic encounter or after they had pursued food items in the drift.

Most hatchery fish moved almost constantly, or remained stationary in other, less energy-saving sites. The tail-beat frequency in such cases was significantly higher than that of hatchery or wild fish using numbered sites. The overall mean tail-beat frequency for stationary hatchery fish was  $1.93 \pm 0.10$  (SE) beats/second ( $N = 34$ ) as compared to  $0.43 \pm 0.03$  beats/second ( $N = 45$ ) for stationary wild fish. The tail-beat frequency of moving hatchery fish,  $2.31 \pm 0.12$  beats/second ( $N = 16$ ) was similar to that of moving wild fish (Table 10).

The hatchery brown trout fed less, and changed position more frequently, than wild fish in both 1979 and 1980 (Table 12). Gape rates were similar for both types of brown trout.

The number of hatchery brown trout declined continuously after they were stocked in observation pools in 1979 and 1980 (Fig. 17). The decline was more rapid in 1979 (when wild trout also decreased in abundance) than it was in 1980. Only 2 of the 179 hatchery fish stocked in the observation pool in 1979 were seen again

in 1980. When seen (once, in early April) they were thin and moving almost continuously. Very few, if any, of the brown trout stocked in 1980 wintered over. In October 1981, when the entire area was censused by electrofishing, none of the 400 hatchery fish stocked in 1979 and 1980 was recovered.

Overall, the behavior of the smaller hatchery brown trout stocked in the spring of 1980 more nearly resembled that of the wild fish than did the behavior of larger fish stocked in late summer 1979.

### Discussion

The foraging behavior of wild brown trout in Spruce Creek reflects the profound effect that current has on the energy fish must expend while living in a lotic environment. The restricted home range of individual fish, the discrete nature of the foraging sites within these home ranges, and the large proportion of time the fish spend stationary in foraging sites suggest that energy expended by the wild brown trout may be a principal determinant of growth rate and population density in Spruce Creek.

### Home Range

The restricted nature of the home range of stream-living trout and juvenile salmon has been inferred by many investigators (Stefanich 1952;



Holton 1953; Miller 1954a, 1957; Newman 1956; Saunders and Gee 1964; Edmundson et al. 1968; Bohlin 1977), but the present study may be the first in which the actual home-range size of free-ranging salmonids has been measured by direct observation. Schuck (1945) reported that most wild brown trout in Crystal Creek, New York, were recaptured by electrofishing in the same sections of stream where they had been originally captured and tagged. He also noted a homing tendency. Many fish caught in an upstream weir during the spawning run later were recaptured in the same section where they had been originally captured, tagged, and released. Miller (1954a) reported a similar homing tendency by wild cutthroat trout *Salmo clarki* removed from their home sites and liberated elsewhere in the same stream, even after several weeks of enforced retention in a new locality. Allen (1951) reported that the majority of wild brown trout captured, tagged, and released in the Horokiwi Stream, New Zealand, were recaptured either at the point where they were initially captured or within a hundred or so meters of it. He noticed that brown trout in different parts of the stream grew at different rates and concluded that the stream population consisted of a linear series of discrete, nonmixing populations. Miller (1957) recorded 67% of recaptures of cutthroat trout in the same pool or within 200 meters of it and concluded that "... each cutthroat trout of Gorge Creek has a home territory not over twenty yards long ... and that the whole life is spent in it." A general lack of movement by yearling and older brown trout also was reported by Solomon and Templeton (1976).

Although the term "home range" is used by many ecologists and behaviorists, there is disagreement over its meaning and how to measure it (Anderson 1982). Burt (1943) defined home range as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young." Wilson (1975) defined it as the area that an animal learns thoroughly and patrols regularly. The home range reported in this study is an estimate of the area an individual wild brown trout used during the time of principal growth, April through November.

There is little doubt that wild brown trout learn the home range thoroughly, and know the location of hiding places or refuge sites. They

proceed directly and with little lost time or energy to such places in deep water, under rocks, or overhanging brush and banks when disturbed from their foraging sites. Similarly they proceed quickly and directly from one discrete foraging site to another. But why do home ranges get smaller as fish get older?

If home-range size were related to food availability, one would expect home ranges to get larger as fish get older. The behavior of the wild brown trout in Spruce Creek suggests that the home ranges of younger fish are larger because older, larger fish are dominant over smaller fish and force them to move about more. Such movement is energetically costly. As a fish grows, its dominance ranking rises, and it is less likely to be displaced from a particular foraging site. One benefit of dominance may be a smaller, less energy-consuming home range.

If one part of the pool yielded a significantly greater amount of food than another, one would expect that the location of the home ranges of the fish would change as they became older and more dominant. But the home ranges of wild brown trout ranging in age from young of the year through 7+ remained substantially the same for as long as three successive summers, even though their rank in the dominance hierarchy rose. When some older fish disappeared (I suspect fish 51 was caught by poachers early in 1979), such "vacancies" were filled by young of the year or yearling fish. Either different parts of the pool do not differ significantly in food availability, as Jenkins (1969) suggested, or the temporal and spatial variability of food supply is so great that the fish cannot detect the difference.

#### *Foraging Sites and Drift-Feeding*

That trout keep to very precise locations has been known for some time (Hoar 1951; Fabricius and Gustafson 1955; Keenleyside 1962; McCormack 1962; Hartman 1963; Elliott 1965; Baily 1966; Frost and Brown 1967; Chaston 1968; Jenkins 1969; Bohlin 1977; Bassett 1978). Indeed, the persistence with which a trout rises time after time in the same spot is at once both the appeal and at times exasperation of the fly fisherman (personal experience). Kalleberg (1958) refers to a Swedish author (Norbäck 1884) as writing "No fish remains for such a long time on its station without moving from there as the river trout ..."



TABLE 7.—Outcome of agonistic encounters between brown trout (identified by number), 1979.

Winning fish	Losing fish																			
	Wild																			
	3	5	7	8	10	11	14	15	23	24	31	32	34	44	51	52	53	54	57	62
Wild																				
3	—					2			1											
5	2	—	2	3								2	2							
7	1	6	—	2					3			11	1	1	1	1				
8				—						1			9			5	4		3	
10				5	—					1	7					4				
11						—			1							3	14			
14	3	1	1	1	1		—		1		1	1	6			2	1			
15		1						—					3		2					
23				1		4			—		2					2	4			1
24				1						—	1								1	
31				4					1		—	3	1			2	12	2	1	
32				39		2				1	1	—		1					2	
34				9		1	1					8	—			6				
44			1										1	—						
51		2	2					1				2	7		—	1	1			
52																—	1			
53				2													—	3		
54																		—		
57																			—	
62																	1			—
Hatchery																				
81				8																
84																	7			
88													2							
95 <sup>a</sup>		5		17					3		3	4	2		4	2	2	1		
Total losses	6	13	6	92	1	9	2	0	10	3	15	31	34	2	7	28	47	6	7	1

<sup>a</sup> Number 95 was assigned to unidentified hatchery brown trout.

In describing the behavior of juvenile Atlantic salmon *Salmo salar* and brown trout in a stream aquarium, Kalleberg (1958) reported "The territorial conditions of the juvenile salmon and brown trout are characterized in a high degree by the fact that each individual possesses within its territory one strongly dominating, strictly localized station. There the fish spends the greater part of its time, from there it defends its territory, and this is the starting point for its feeding excursions."

There is considerable variance and uncertainty in the literature about the meaning of such terms as "station" (Kalleberg 1958; Keenleyside and Yamamoto 1962; McCormack 1962; Bassett 1978; McNicol and Noakes 1981), "home station" (Slaney and Northcote 1974), "position" (Keenleyside 1962; Jenkins 1969), "holding position" (Feldmeth and Jenkins 1973), "microhabitat" (Baltes and Vincent 1969), "lie"

(Frost and Brown 1967), "focal point" (Griffith 1972, 1974; Fausch 1981; Fausch and White 1981), and "territorial focal point" (Everest and Chapman 1972).

Explanations for why salmonids in streams exhibit such localized behavior usually are based on inferences that the locations chosen enable the fish to capture food efficiently and to avoid predation. In this study, I distinguished between those locations the wild brown trout used when drift-feeding (foraging sites), and those sites used when not feeding (refuge sites). The energy-saving utility of foraging sites is evident from the comparative tail-beat frequencies when the fish are waiting in the site, and from the time and effort required to return to the site after each feeding excursion. While the gross location of foraging sites may be influenced by drift patterns (Jenkins 1969), the lack of correlation between site utilization and feeding



TABLE 7.—*Extended.*

Winning fish	Losing fish				Total wins
	Hatchery				
	81	84	88	95 <sup>a</sup>	
Wild					
3					3
5				6	17
7					27
8				2	24
10					17
11					18
14					19
15				3	9
23					14
24					3
31				9	35
32				1	47
34					25
44					2
51					16
52					1
53					5
54					0
57					0
62					1
Hatchery					
81	—			2	10
84		—			7
88			—	2	4
95 <sup>a</sup>		6		58	105
Total losses	0	6	0	83	409

rates, dominance ranking, and distance to cover suggests that drift patterns, if present, have little effect on site selection.

Another benefit associated with foraging sites may be that the brown trout use the energy in the current to intercept food in the drift. By a relatively small movement of pectoral fins and a flick of the caudal fin, the fish's head is raised into the overhead slipstream. The movement, as revealed in slow-motion videotapes and cinematography suggests that the differential flow over the head and anterior part of the body produces a Bernoulli effect, aiding the fish to capture food with less energy. Energy maximization should be a powerful selection pressure (Fausch and White 1981; Bachman 1982). I suggest that foraging sites are chosen primarily for their energy-saving utility and that at high population densities, foraging sites are a limiting factor. Agonistic encounters associated with foraging sites but not with refuge sites in Spruce Creek support this hypothesis.

Selectivity and size-dependent feeding in a lotic environment has been demonstrated in the case of brook trout (Allan 1978, 1981), juvenile coho salmon *Oncorhynchus kisutch* (Dunbrack and Dill 1983), rainbow trout (Metz 1974; Bisson 1978), and brown trout (Nilsson 1957; Elliott 1967a; Ringler 1979) from stomach-sample analyses. Butler and Hawthorne (1968) reported that large brown trout frequently tolerate smaller trout downstream of them, but never upstream. McNicol and Noakes (1981) showed that the area in which agonistic behavior of juvenile brook trout took place was chordate in shape with the resident stationed at the downstream end facing into the current. A possible explanation for size-dependent food selectivity and the age-dependent decline in feeding rate of the wild brown trout in Spruce Creek is that older, larger fish may pass up smaller items in the drift that would not compensate for the energy expended in capturing them.

#### *Dominance Hierarchies*

In studies in which the relationships of neighboring brown trout have been directly observed (Jenkins 1969; Bassett 1978; McLaren 1979; present study), dominance was correlated with the age (size) of the fish, but little or no prior residence effect was evident. Neither was there a clear correlation between dominance and position choice, feeding rate, agonistic encounter rate, or distance to cover. In short, the dominant individual appears to have no preferential access to any "best area." So what purpose does the linear hierarchy serve?

The establishment of hierarchies should minimize energy expenditure in the long run. Brown trout normally feed on drift items one by one. If two or more fish were to pursue the same item, at most only one would obtain a benefit to offset its cost. In a lotic environment, the energetic cost associated with drift-feeding is considerable. It is apparently less costly to periodically engage in dominance contests than to scramble for food as each item drifts into view. This is, of course, similar to the arguments used by MacArthur (1972) and Wilson (1975) in showing that territoriality is less costly than pure scramble in defense of food resources.

Li and Brocksen (1977) found that certain subdominant rainbow trout grew faster than the alpha (dominant) individual. A possible ex-



TABLE 8.—Outcome of agonistic encounters between brown trout (identified by number), 1980.

Winning fish	Losing fish																	Total wins			
	Wild													Hatchery							
	3	8	10	11	14	15	30	31	32	36	37	53	54	57	91	92	93		94	95 <sup>a</sup>	96
Wild																					
3	—											1							1		2
8		—		2			3		8			8		2	3	1			4		31
10		5	—						2												7
11	1			—						3		1		1	1			1	3	1	12
14	1			3	—														1		5
15	1	1				—						3			5	1		1	12		24
30		1					—				1										2
31		8					9	—	18	20	1		4	7	3			1	4		75
32								1	—	1		3	1	4	1				1		12
36							4			—			1								5
37							1				—										1
53							3				1	—							5		9
54										2		1	—						1		4
57		1					3		1	8	1	3	5	—	4		3		1	2	33
Hatchery																					
91							2		2	9	8	1		9	—						31
92			2				1			1	4	1			1	—			1		11
93										2							—		1		3
94					1													—			1
95 <sup>a</sup>	1	3		1			1			1			1						21		29
96												4								—	4
97																		1	1	1	3
Total losses	4	19	0	8	1	0	27	1	31	47	16	26	12	23	18	2	3	4	57	4	304

<sup>a</sup> Number 95 was assigned to unidentified hatchery brown trout.

planation, but by no means the only one, is that in the confined space of an aquarium a dominant (largest) fish expends too much energy when repeatedly confronted by roving subdominants. At Spruce Creek, higher-ranking wild brown trout, after having repeatedly run off, or defeated, lower-ranking individuals, occasionally did not return immediately to the site at which the agon was initiated, but rather moved to another foraging site. Although anecdotal, such observations suggest that the dominant fish may have moved to another site simply because it was too costly to continue to use the former site.

I believe that agonistic behavior at foraging sites results in the establishment of dominance hierarchies, and that the behavior, when observed over a relatively short period of time gives the impression of territoriality.

#### *Territoriality*

Noble's (1939) definition of a territory, "any defended area," is in common use today (Ito 1978), although Wilson (1975) defines it some-

what differently by emphasizing exclusivity—"An area occupied more or less exclusively by an animal or group of animals by means of repulsion through overt defense or advertisement." Davies (1978) gives a much broader definition, and recognizes a territory whenever individual animals or groups are spread out more than would be expected from a random occupation of suitable habitats.

Hixon (1980), on the other hand, takes a much narrower view in the definition of territory as "the nearly exclusive access to and utilization of food resources within a mobile animal's home range as a direct result of that animal's aggressive and/or ritualized expulsion of individual food competitors."

Because salmonids are at times difficult to observe directly and identify individually, indirect methods usually have been used to document territoriality. Many authors simply infer territoriality from the observations of stationariness or limited home range (Allen 1951; Fabricius and Gustafson 1955; Newman 1956; Latta 1965; Burnet 1969; Le Cren 1973; Bohlin 1977, 1978).



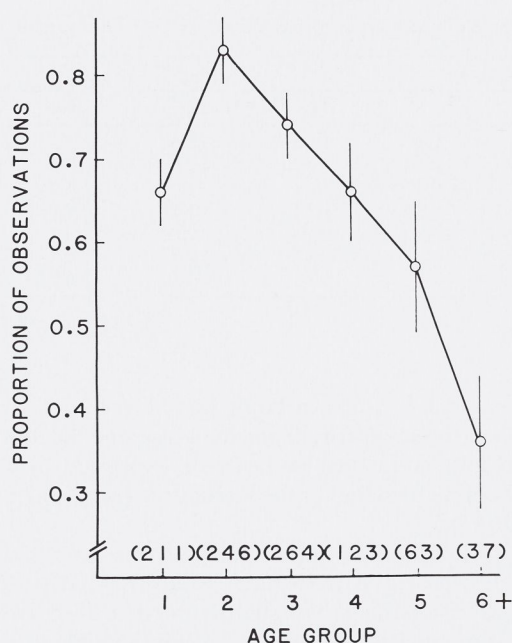


FIGURE 16.—Mean proportion of daily scan observations in which individuals of different age groups were sighted, given that the individual was observed at least once during an observation day; 95% confidence interval is shown by vertical bars. Number of observations for each age group is in parentheses.

Others would maintain that aggressive behavior coupled with stationariness implies territoriality (Stringer and Hoar 1955; Lindroth 1956; Moyle 1969; Slaney and Northcote 1974; Dill 1978). Some make little distinction between territoriality and dominance (Chapman 1962; Keenleyside and Yamamoto 1962; Symons 1971; Li and Brocksen 1977), and Chapman (1966) implied that territories develop in riffles but hierarchies in pools. Noakes (1978), in a general review,

TABLE 10.—Tail-beat frequencies of wild brown trout during various activities in Spruce Creek.

Activity	Mean tail beats per second $\pm$ SE	Number of observations
Sit and wait	0.4 $\pm$ 0.0	45
Return from midwater feed	1.8 $\pm$ 0.7	11
Return from surface feed	2.3 $\pm$ 0.7	43
Stationary swimming near surface	3.0 $\pm$ 0.6	5

suggested that dominance may grade into site-dependent dominance, territoriality, or both, a concept described as scaling in aggressive behavior by Wilson (1975).

Perhaps no other paper is more frequently cited in regard to territoriality of salmonids than Kalleberg's of 1958. It was the first study in which an attempt was made to directly observe and measure the size of individual territories. Kalleberg estimated the size of territories of juvenile Atlantic salmon in a stream aquarium by the distance at which individuals responded aggressively to neighbors and dummies and by "dividing a representative part of the bottom surface by the number of fishes which there defend territories." He implied that each individual had only one station but allowed the possibility of "secondary centres." Not all Atlantic salmon occupied fixed stations. More of them "defended" territories when the water velocity in the tank was increased, and the addition of large rocks produced a similar increase in the number of "territorial" fish. He attributed this change to "visual isolation," although figures accompanying his article show that many of the juvenile salmon had stations on top of the large rocks.

TABLE 9.—Activity durations for wild brown trout in Spruce Creek. Data are mean seconds  $\pm$  SE, derived from analysis of video tapes.

Activity	Number of observations	Pursuit time	Time to return	Total
Feeding				
Surface	39	1.0 $\pm$ 0.1	6.0 $\pm$ 0.3	7.0 $\pm$ 0.4
Midwater	33	1.0 $\pm$ 0.1	3.8 $\pm$ 0.4	4.9 $\pm$ 0.5
Bottom	13	1.0 $\pm$ 0.1	2.7 $\pm$ 0.5	3.8 $\pm$ 0.5
False feed	24			2.5 $\pm$ 0.3
Agonistic encounters	21			13.7 $\pm$ 1.1



TABLE 11.—Age-related distribution of activity times (%) for wild brown trout in Spruce Creek, 0900–1900 hours.

Activity	Age group						Weighted mean <sup>a</sup>
	1	2	3	4	5	6+	
Pursuit	3.9	3.4	2.9	2.8	1.8	1.0	3.1
Return to site	10.1	9.5	7.8	7.7	4.9	2.6	8.4
Position change	1.3	1.7	1.7	0.7	1.1	1.0	1.4
Agonistic encounters	0.6	0.8	0.8	0.9	1.4	1.2	0.9
Gape	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Sit and wait	84.0	84.5	86.8	87.8	90.8	91.1	86.2

<sup>a</sup> Weighted for age group.

I believe that the behavior described by Kalberg (1958) can be more easily and parsimoniously explained as an energy-minimizing response. When water velocities are high, fish cannot afford to pursue food or attack intruders at as great a distance as when velocities are low. The addition of large rocks may well have simply added more energy-saving sites. Stationariness accompanied by aggressive behavior, I believe, is not sufficient to define territoriality.

Ito (1978) and Noakes (1978) distinguished between territoriality and hierarchies on the basis of prior residence. Noakes (1978) stated, "We must have individual identification of the fish within a group, and evidence that dominance is independent of location within the study area, before reasonably concluding that a dominance hierarchy is present." and Ito (1978) stated, "... in a conflict over a territory the characteristic of territoriality is, that, unlike social hierarchies seen within groups of non-territorial species, the territory holder wins the fight as a rule even if he is smaller than the intruder. This is called the effect of prior residence." If prior residence can be considered to be a formal test of territoriality, then the wild brown trout at Spruce Creek were not territorial. That the outcome of agonistic encounters among wild trout was not site-dependent is attested to by the remarkably linear social structure observed, with few reversals or ambiguities, and the stability of the structure from year to year. The introduction of hatchery brown trout further demonstrated that no prior resident effect was evident and that the outcome of agonistic encounters was primarily a function of size.

Bohlin (1977) claimed that resident age-1+ wild brown trout had an owner's advantage over

wild age-1+ brown trout introduced into an experimental area from downstream, but the results might just as easily be explained by a homing tendency of the introduced fish (Schuck 1945).

Nice (1941) defined six major types of territory according to the function involved. Wilson (1975) modified these slightly and described five types labeled, A through E, that depended on various mixes of mating, nesting, resting, and foraging activities. Ito (1978) introduced a new Type F territory, a defended area in which the food supply is guaranteed, whether for reproduction or not. Wilson (1975) disagreed with those who would define territory in terms of economic function (Pitelka 1959), and sided with those who define territory by the mechanism through which exclusiveness is maintained.

All of the brown trout in Spruce Creek used more than one foraging site in a day and none of the sites was used exclusively by only one fish. No fish had an exclusive home range or foraging site, so neither the home range nor the area surrounding the foraging sites would pass the exclusivity test for territoriality.

One could argue, of course, that each foraging site held by the fish is a "partial" (Greenberg 1947), "floating" or "spatio-temporal" territory (Wilson 1975). One could add to the confusion by coining yet another term "pseudo-territory." I suggest instead that none of these terms confers any more information than merely stating that foraging sites are energetically efficient and that the agonistic behavior associated with foraging sites is a cost-minimizing phenomenon. I suggest that the term territoriality may be meaningless as generally applied to stream-living salmonids (with the possible exception of the ayu *Plecoglossus altivelis*: Kawa-



TABLE 12.—Comparative activity of wild and hatchery brown trout in Spruce Creek, 1979 and 1980.

Activity	Type of fish	Mean number per 15 minutes $\pm$ SE	Data transformation	Number of 15-minute observation periods	<i>P</i> ( <i>t</i> -test)	Proportion of non-zero observations	<i>P</i> (binomial)
<i>Late summer 1979</i>							
Feeding Surface	Wild	4.7 $\pm$ 1.0	Log <sub>e</sub>	63	<0.01	0.70	0.01
	Hatchery	0.3 $\pm$ 0.1		62		0.16	
Midwater	Wild	3.4 $\pm$ 0.5	Log <sub>e</sub>	63	>0.20	0.70	0.01
	Hatchery	1.8 $\pm$ 0.4		62		0.46	
Bottom	Wild	1.0 $\pm$ 0.2	Log <sub>e</sub>	63	0.06	0.41	0.01
	Hatchery	0.3 $\pm$ 0.1		62		0.16	
Total	Wild	9.2 $\pm$ 1.2	Log <sub>e</sub>	63	<0.01	0.89	0.01
	Hatchery	2.4 $\pm$ 3.5		62		0.60	
Agonistic encounters	Wild	1.7 $\pm$ 0.4	Log <sub>e</sub>	63	0.06	0.43	0.10
	Hatchery	3.4 $\pm$ 0.7		62		0.57	
Gape	Wild	0.4 $\pm$ 0.1	Square root	63	>0.20	0.81	>0.20
	Hatchery	0.3 $\pm$ 0.1		62		0.84	
Moves	Wild	3.1 $\pm$ 0.6	Log <sub>e</sub>	63	<0.01	0.62	0.06
	Hatchery	10.4 $\pm$ 2.1		62		0.77	
<i>Spring 1980</i>							
Feeding Surface	Wild	9.4 $\pm$ 0.8	Square root	152	0.03	0.86	0.01
	Hatchery	4.8 $\pm$ 0.6		98		0.61	
Midwater	Wild	8.2 $\pm$ 0.8	Log <sub>e</sub>	152	<0.01	0.89	0.04
	Hatchery	4.2 $\pm$ 0.4		98		0.79	
Bottom	Wild	1.8 $\pm$ 0.2	None	152	>0.20	0.62	0.04
	Hatchery	1.6 $\pm$ 0.3		98		0.49	
Total	Wild	19.4 $\pm$ 1.3	Square root	152	<0.01	0.98	0.02
	Hatchery	10.6 $\pm$ 0.9		98		0.87	
Agonistic encounters	Wild	1.7 $\pm$ 0.2	None	152	>0.20	0.53	>0.20
	Hatchery	2.2 $\pm$ 0.6		98		0.46	
Gape	Wild	0.8 $\pm$ 0.1	None	152	0.11	0.55	0.01
	Hatchery	0.6 $\pm$ 0.1		98		0.36	
Moves	Wild	3.2 $\pm$ 0.4	Log <sub>e</sub>	152	0.01	0.60	>0.20
	Hatchery	4.4 $\pm$ 0.7		98		0.53	

nabe 1969) and that it carries with it certain connotations that so far have not been supported by field observations.

#### Growth

We would expect to find the reproductive success of salmonids to be highly correlated with size. Larger fish have more and larger eggs (Frost and Brown 1967; Weatherly and Rogers 1978), and larger eggs produce larger young that, in turn, have better growth and survival (Lagler et al. 1962; Frost and Brown 1967; Bagenal 1969). Size is also an important factor in competition among males during the spawning

season (Frost and Brown 1967; Butler and Hawthorne 1975; personal observation). Consequently, there should be a strong selective pressure for rapid and sustained growth among salmonids.

But growth typically is found to be asymptotic, the upper limit of growth differing from one stream to another. This leads us to search for physiological and environmental factors that determine growth rates and upper limits to growth.

In streams such as Spruce Creek, certain species of salmonids may derive the majority of their food from drift (Müller 1954; Nilsson 1957;



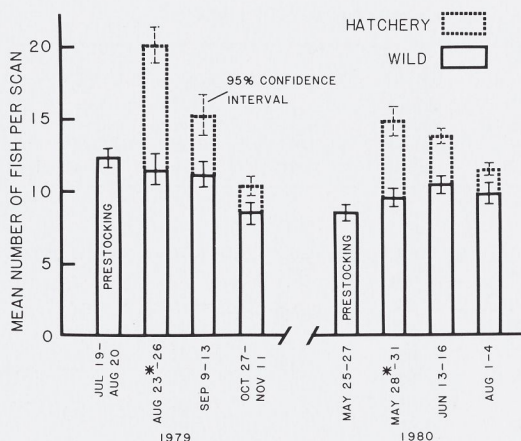


FIGURE 17.—Mean number of wild and hatchery brown trout seen during hourly scan observations in 1979 and 1980. Stocking dates (\*) were August 23, 1979, and May 28, 1980.

Elliott 1967b; Waters 1969; Griffith 1974). Although the numbers and biomass of drift organisms in streams are spatially and temporally quite variable (Elliott 1967b; Lehmkuhl and Anderson 1972; Reisen and Prins 1972; Waters 1972; Bisson 1978) it appears that the mean amount of drift that passes a particular point in a stream is, over the long run, a linear function of the velocity at that point (Elliott 1967b; Chapman and Bjornn 1969). The metabolic rate, or amount of energy expended per unit time by salmonids, on the other hand, is an exponential function of swimming speed (Brett 1964; Rao 1968).

I previously showed (Bachman 1982) that these environmental and physiological constraints set a size-dependent optimum velocity for drift-feeding fish. At the optimum velocity, growth rate should be maximal. According to this model, larger drift-feeding fish should grow faster in slower water, and a fish that remains a drift feeder should ultimately grow to a size at which the energy in the drift just equals the energy expended in capturing food, producing gametes, and reproductive behavior.

As a first approximation, then, the growth rate of individual fish should be determined by the differential energy between that obtained from the drift in a fish's home range and the energy it expends to obtain it. Because drift densities vary from stream to stream and from place to place within a stream, and because many

salmonids spend most of their lives in one small section of a stream (Schuck 1945; Allen 1951; Miller 1954a, 1957; present study), different places should grow different size fish and at different rates. Brown trout (Allen 1951), brook trout (Cooper et al. 1962), and cutthroat trout (Cooper 1970) have all been reported growing faster in the lower parts of a stream than in the upper parts.

It may be that large trout are repeatedly captured at the same places in a stream because those places grow larger fish rather than attract larger fish. This idea is supported by the observation that when a few large brown trout disappeared from the observation area in the spring of 1980 (there was some evidence of poaching at the time) the feeding sites formerly occupied by an age-5 fish (number 51) subsequently were occupied by a yearling.

If population densities, as I have suggested, are determined primarily by the number of suitable foraging sites, and the growth rates are determined by the energy differential at those foraging sites, what might be the density effect on growth?

If the rate at which drift-feeding fish take food from the current is very much smaller than the rate the food enters and leaves the water from the surface and the bottom, growth rates should be independent of population density. Although few data exist on the rates food enters and leaves the drift, because such rates are so hard to measure, there is evidence of density-independent growth by coho salmon (Chapman 1965), brook trout (Cooper et al. 1962), and brown trout (Mortensen 1982).

#### Gaping

The gape reflex of wild and hatchery brown trout appears to be a comfort movement induced by the buildup of  $\text{CO}_2$  in the bloodstream. Two factors theoretically would affect blood  $\text{CO}_2$  concentrations, metabolic rate and  $\text{CO}_2$  concentrations in the water. The positive correlation of gape rate with temperature, the high gape rates in summer, and the sharp rise in gape rate in mid-afternoon appear to reflect the temperature effect on metabolic rate. The morning decrease in gape rate probably reflects a drop in dissolved  $\text{CO}_2$  in the water associated with photosynthetic activity of macrophytes and algae in the stream. The temporal gaping pattern evident by both wild and hatchery brown



trout suggests that this may be a fruitful area for further research.

#### *Hatchery and Wild Trout Compared*

The poor survival of hatchery trout in streams is well documented (Hoover and Johnson 1938; Hazzard and Shetter 1939; Shetter and Hazzard 1941; Needham and Slater 1944, 1945; Schuck 1945, 1948; Smith and Smith 1945; Shetter 1947; Cooper 1953, 1959; Miller 1958; Mason et al. 1967; Millard and MacCrimmon 1972), but there is no consensus as to the cause. Schuck (1948) listed ten possible causes, ranging from environmental factors such as insufficient food, high water temperature, and predation to management practices including planting methods, hatchery diets, lack of exercise in the hatchery, and domestication. Miller (1952, 1958) attributed weight loss and mortality of hatchery-reared cutthroat trout stocked in Alberta streams to competition with wild trout and showed that hatchery fish stocked in a stream that contained wild fish had higher lactic-acid concentrations in the blood than did hatchery cutthroat trout not in "competition" with wild fish. Nielsen et al. (1957), on the other hand, reported that differences in stocking densities of hatchery rainbow trout had no effect on the survival of the stocked fish and concluded that competition with wild brown trout was *not* a cause of mortality among hatchery-reared trout. Miller (1954b) and Vincent (1960) suggested that selection in the hatchery produces domesticated fish that cannot survive well in streams.

In work with juvenile Atlantic salmon, Fenderson et al. (1968) proposed that unnaturally high aggressiveness in hatchery stocks may contribute to mortality through loss of feeding time, excessive expenditure of energy, and increased exposure to predators. Jenkins (1971) came to much the same conclusion, suggesting that the behavioral patterns of domesticated trout, successful in a crowded hatchery raceway, are wasteful of energy and ill-adapted to the conditions in a natural environment. Even when the return of stocked trout to anglers is high, and a large fraction are taken within a few weeks of planting, the natural mortality rate (or "unaccounted mortality"), as reflected in the number of trout lost due to causes other than angling, may be very high (Butler and Borgeson 1965).

The results of my study at Spruce Creek support the hypothesis that a contributing cause of mortality among hatchery trout is excessive expenditure of energy. The hatchery brown trout moved more frequently, were less likely to use energy-efficient foraging sites, and engaged in more agonistic encounters than the wild brown trout. Although hatchery brown trout won as many agonies as they lost, they were less likely to return to the location where the agony was initiated than were wild fish. The lack of identification with any particular geographic location and the attendant failure to become integrated into a long-term social structure also must be costly to hatchery fish.

Hatchery brown trout fed much less than did wild brown trout, a factor that would aggravate the already adverse energy balance. In contrast, McLaren (1979) reported that wild brown trout from Spruce Creek, transported, tagged, and stocked in hatchery raceways, fed less frequently than hatchery brown trout subjected to the same treatment. This suggests that wild brown trout may be more stressed by handling and new surroundings than hatchery brown trout.

The reason the hatchery fish in my study fed less than the wild fish may be that it takes a considerable time for hatchery brown trout to learn to feed on natural food and some may never learn. Elliott (1975) showed that some hatchery brown trout refused to eat or took only a small number of natural food items in a feeding experiment. Ersbak and Haase (1983) found that wild brown trout ate nearly twice as much food as hatchery-reared brook trout in McMichael Creek, Pennsylvania, and concluded that the stocked brook trout were unable to obtain sufficient food for survival in the stream they studied.

Other factors that may account for poor survival of hatchery trout in streams are size and condition. Klak (1941), Needham and Slater (1945), Miller (1952, 1954b, 1958), Reimers (1963), Hunt and Jones (1972), and Ersbak and Haase (1983) all reported a decline in condition factor of hatchery trout stocked in streams. Ersbak and Haase (1983) also showed that the higher the coefficient of condition when stocked, the faster it declined. According to the energy-balance model for drift-feeding salmonids that I developed (Bachman 1982), there is an upper size limit that a drift-feeding salmonid can attain in a particular environment and population

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density has little or no effect on that limit. The hatchery brown trout in Spruce Creek were, like the wild brown trout, drift feeders. One reason many hatchery trout die may be that they are too big for the stream in which they are stocked. It seems unreasonable to expect a 35-cm hatchery trout to survive in a stream where the average wild trout rarely exceeds 30 cm.

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## Foraging Behavior of Free-Ranging Wild and Hatchery Brown Trout in a Stream<sup>1</sup>

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### Abstract

Wild brown trout *Salmo trutta* in a fertile, high-conductivity stream in central Pennsylvania were observed from camouflaged towers for three consecutive years in order to quantify the diurnal feeding and social behavior of undisturbed adults. The foraging behavior observed was characterized in general as one of net energy maximization effectuated principally by cost minimization. Individuals ranging in age from young of the year to 8 years spent 86% of foraging time in a sit-and-wait search state, used discrete, energy-saving foraging sites year after year, and fed mainly off drift, taking less than 15% of their food items directly off the bottom. Feeding rates decreased with age, were highest in spring and fall, and showed little effect of time of day except for short peaks at dusk in May and June. The home range of most individuals was established in the first or second year of life and changed little thereafter. The mean size of the home range of individuals was 15.6 m<sup>2</sup> and decreased slightly during the first 4 years of growth. No individual had exclusive use of any home range and no clearly defined territory could be described for any fish. Rather, the social structure evidenced is best described as a cost-minimizing, size-dependent, linear dominance hierarchy of individuals having overlapping home ranges. There was no apparent correlation between dominance and site selection with respect to distance to cover or feeding rate. Use of overhead cover ranged from 17% or less of daylight hours for wild brown trout of age-group 2 to no more than 43% for age-group 5. Length was asymptotic at 40 cm. A rectangular hyperbola described well the overall growth curve of fish in this population, half of the asymptotic length being attained at the age of 23 months. Hatchery brown trout, introduced for experimental purposes, fed less, moved more, and used cost-minimizing features of the substrate less than wild trout. It is postulated that high energy cost is a major cause of mortality among hatchery-reared brown trout stocked in streams, that at high population densities foraging sites are limiting factors, and that growth rate of drift-feeding salmonids is density-independent.

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Many of our ideas about the social structure and population dynamics of salmonids in streams

are based on studies of juveniles in laboratory conditions and spot samplings of natural populations (Northcote 1969; Butler 1974; Gerking 1978). Few studies have included direct observation of undisturbed wild populations and those that have, have been qualitative in nature for the most part (Fabricius and Gustafson 1955; Newman 1956; Horton 1961; Keenleyside 1962; McCormack 1962). Recently, Jenkins (1969), Bassett (1978), and McLaren (1979) studied the

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social structure; Baldes and Vincent (1969) the microhabitat; Devore and White (1978) the response to cover stimuli; and Ringler (1979) selective feeding of wild brown trout *Salmo trutta* constrained in artificial or simulated stream channels.

Griffith (1972) and Fausch and White (1981) used mask and snorkel to observe wild trout populations in natural streams and to measure the microhabitat used by individuals, but, except for this study, I have been unable to find in the literature any quantified, long-term observations of the social structure and feeding behavior of unconstrained wild populations.

The density-regulatory effect of social behavior among salmonids in streams has received considerable attention (Chapman 1966; Chapman and Bjornn 1969; McFadden 1969) but remains somewhat equivocal. The regulatory mechanism generally invoked is territoriality, and despite (or perhaps because of) the lack of direct observational data, the concept of territoriality among stream-living salmonids is virtually dogmatic.

An increasing number of authors have begun to question the concept of territoriality, especially as it applies to the nonreproductive phase of stream-living salmonids. Allen (1969), in attempting to correlate territory size with the size of fish, remarked that he was able to find little direct measurement of territory size in the scientific literature. Jenkins (1969) reported that strictly territorial individuals were rare, and later (1971), in discussing territoriality, commented, "I find a simple, precise form of social density control difficult to visualize in such a social framework." Concerning the possibility of territoriality being an artifact of experimental design, Hoar (1969) warned, "... laboratory studies can be misleading as well as revealing in our attempts to understand the ecology of fishes." Butler (1974) described the behavior of salmonids in terms of a "social force field" (McBride 1964) and suggested that wild adult trout, in contrast to juveniles, had "no territory as understood in the traditional sense." Later, Ito (1978), in discussing territory stated, "Under special circumstances such as fish kept in an aquarium, the defense of an area observed will not constitute territoriality unless it has significance in the *normal* life of that species in the field." Noakes (1978), in commenting on the distinction between territoriality and domi-

nance-subordination relationships stated, "We must have individual identification of the fish within a group, and evidence that dominance is independent of location within the study area, before reasonably concluding that a dominance hierarchy is present." And, further, "We should exercise caution in ascribing consequences to, or even inferring the existence of territoriality without direct confirmatory observation."

A basic tenet of behavioral ecology is that animals behave as they do because the behavior in question enhances the reproductive success of the individual exhibiting the behavior (Pyke et al. 1977; Krebs and Davies 1978). That is, the behavior is adaptive. The interesting questions concerning adaptation often concern how animals respond to different aspects of the environment (Maynard Smith 1978). If we are to understand the mechanisms by which food and space regulate the growth and distribution of salmonids in streams, we need to understand how an individual animal responds to environmental variables in order to maximize its reproductive success. The purpose of my 3-year study was to acquire such understanding of an undisturbed population of wild brown trout and to analyze the extent to which such concepts as dominance and territoriality pertain to free-ranging populations.

A second objective of the study was to quantify the differences in behavior of wild and hatchery-reared brown trout and to investigate the possible causes of poor survival of hatchery brown trout in streams.

#### Study Site

Spruce Creek is a hard-water stream rising from limestone springs near Rock Springs, Huntingdon County, Pennsylvania and flows generally southwest through farmland and hardwood forest for 15.5 km to its confluence with the Little Juniata River at the town of Spruce Creek. Fed by two major tributaries, Halfmoon Creek and Warrior's Mark Creek, it varies in width from approximately 5 m at its confluence with Halfmoon Creek to 12 m at its mouth. Although subject to flooding after severe summer thunderstorms and after winter rains when the ground is frozen, the stream drops quickly after such infrequent episodes, and has a fairly steady flow year round (McFadden and Cooper 1964).

In an ecological comparison of six brown trout



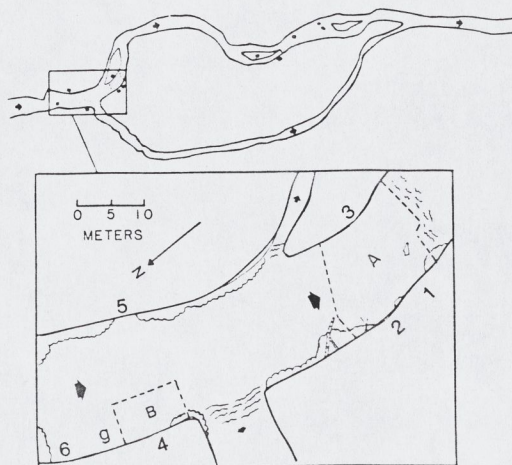


FIGURE 1.—The Spruce Creek Experimental Fisheries Area. The enlargement shows locations of observation areas A and B, observation towers 1–6, and water-level gauge (g). Arrows on stream indicate direction of water flow.

populations in Pennsylvania, Spruce Creek had the greatest biomass of brown trout: 126 kg/hectare (McFadden and Cooper 1962). The specific conductance is near 285  $\mu$ mhos/cm (McFadden and Cooper 1964; McLaren 1970). Typical values of total nitrate and total phosphorous are 1.6 mg/liter and 0.05 mg/liter, respectively.

The Spruce Creek Experimental Fisheries Area, site of this study, is owned by the Pennsylvania State University and was managed by the Pennsylvania Cooperative Fishery Research Unit for catch and release fly fishing (only) from April 1968 through this study's completion in October 1981. It is located approximately 1 km from the confluence with the Little Juniata River. Within the study area, the stream averages 12.8 m wide, is 1,062 m long, has a 0.8% gradient and a surface area of 1.3 hectares (McLaren 1970) (Fig. 1). The most abundant salmonid in the area is the brown trout (Beyerle and Cooper 1960; McLaren 1970). An electrofishing census (April 28–May 1, 1975) yielded a brown trout standing-crop estimate of 145 kg/hectare. Of 1,427 brown trout captured, less than 5% of the yearling and older fish were over 32 cm total length (Fig. 2). Because young of the year emerge from the gravel in Spruce Creek over an extended period from late March through early May, and are only about 2 cm long when they emerge (Beyerle and Cooper

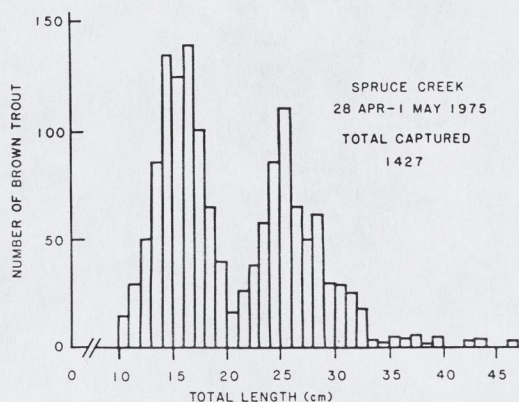


FIGURE 2.—Length frequencies of 1,427 yearling and older brown trout captured by electrofishing in the Spruce Creek Experimental Fisheries Area, April 28–May 1, 1975. The first peak is composed of age group I, second peak, age groups II and older.

1960), they were poorly represented in the censusing techniques employed, and not included in the 1975 census figures.

The brown trout in the Experimental Fisheries Area are almost exclusively of wild origin. The stream is not stocked by the Pennsylvania Fish Commission except for a short stretch approximately 14 km upstream of the study area. McLaren introduced hatchery-raised brown trout into the research area in 1969 and again in 1971 for experimental purposes but they survived poorly (McLaren 1970, 1979). Private landowners and fishing clubs along the stream stock some brown trout but no trout of recent hatchery origin were found in the 1975 census. These would have been recognized by their comparatively pale coloration and abraded fins.

Other salmonids are rare in the area. Only 17 rainbow trout *Salmo gairdneri* and 3 brook trout *Salvelinus fontinalis* were captured in the 1975 census. Other fish species in the area include the white sucker *Catostomus commersoni*; the tessellated darter *Etheostoma olmstedii*; the slimy sculpin *Cottus cognatus*; and the cyprinids *Rhinichthys atratulus*, *Rhinichthys cataractae*, *Exoglossum maxillingua*, *Notropis cornutus*, and *Pimephales notatus* (Beyerle and Cooper 1960).

The largest pool in the Experimental Fisheries Area is located near the upstream end where the stream splits into three channels (Fig. 1). This pool contained an estimated population of 200 yearling and older wild brown trout in





FIGURE 3.—Observation area A (foreground), towers 1 and 2, at left. Tower 4, by observation area B, is upstream and to the right. Natural vegetation and burlap shielded observers.

1975. The pool, 90 m long from riffle to riffle and 15.2 m wide, has a surface area of approximately 0.14 hectares. The mean summer low flow through the pool at water gage height 0.15 m is 2.8 m<sup>3</sup>/second. No fishing was permitted in this pool during the period of the study (June 1977 through October 1981).

#### Methods

Brown trout were observed from six camouflaged portable aluminum radar towers erected along the large pool in the upstream part of the Experimental Fisheries Area (Fig. 1). Each tower consisted of two sections that raised the height of eye 1.8 m and 3.3 m above water level. Burlap on the towers and natural vegetation broke the silhouette of observers and permitted entry to the towers without disturbance of the fish (Fig. 3). A wooden roof and visor shielded observers and equipment from rain and prevented reflected sunlight from alarming the fish.

During a pilot study in 1977, I discovered that I could identify individual brown trout by their spot patterns and that the location of individuals within the large pool was very predictable from day to day. I also discovered that the "lies" of the fish (later referred to as foraging sites) were so precise and the manner in which different fish used them so similar that they could be used as spatial references for behavioral observations.

I first observed the brown trout from three towers along each side of the pool. After I de-

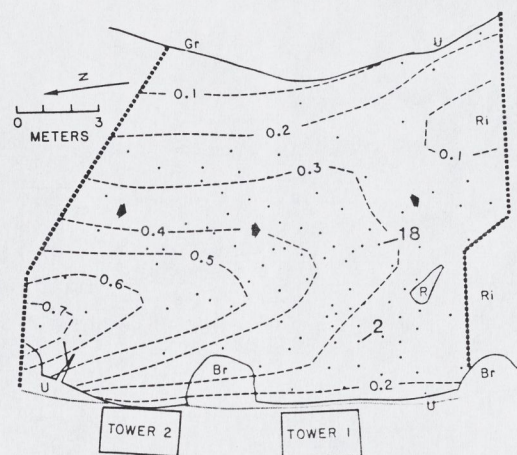


FIGURE 4.—Map of 96 numbered foraging sites in observation area A and mean depth contours in meters. Sites 2 and 18 are labelled. Arrows indicate direction of water flow; R = rock, Br = brush, Gr = gravel bar, U = undercut bank, Ri = riffle.

termined that the behavior of the brown trout was qualitatively the same in all parts of the pool, I selected the tail of the pool (observation area A) for detailed quantitative observation because (1) the surface of the water there was relatively free of ripples, (2) the water shoaled off toward the end of the pool, giving a range of depths in which to observe the fish, and (3) there was less glare and better lighting there. From towers 1 and 2, I also could see some brown trout in riffle habitat (Fig. 4). I constructed a montage of the observation area by fitting together photographs of the bottom. Each foraging site, marked by the location of the eye of the fish occupying it, was assigned a number and located on the montage. The observation area was measured and each foraging site was assigned grid coordinates for subsequent computer analysis.

#### Identification of Fish

I identified each brown trout in the observation area by the spot pattern on the left side of the body below the dorsal fin (Figs. 5 and 6). Identification and observation were facilitated by 7 × 35 and 7 × 50 binoculars fitted with polarizing filters.

The fish were photographed from the towers through a 400-mm f/5 telephoto lens fitted with extension tubes to reduce the minimum focus



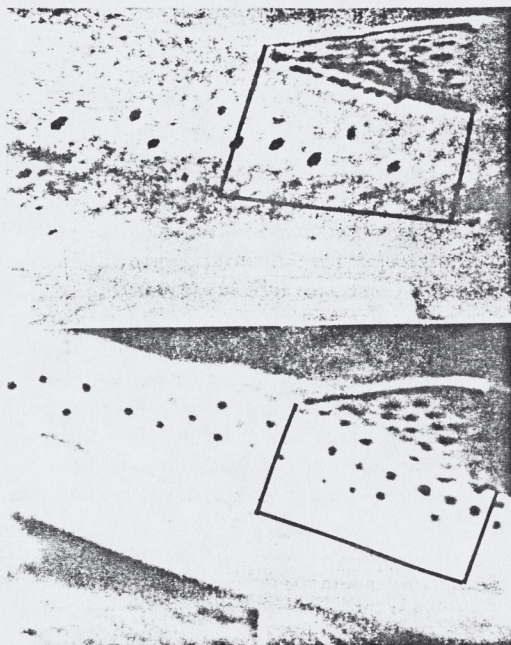


FIGURE 5.—Spot patterns of wild brown trout 31 (top) and wild brown trout 32 (bottom) within rectangular reference areas between the dorsal fin and lateral line.

distance. Kodacolor 35 mm, ASA 400 film gave best resolution, contrast, and color tone. A complete photographic identification file of all fish observed was assembled to ensure positive identification. Wild brown trout were assigned numbers 1 through 79 and hatchery brown trout 80 through 97. Gaps in number series reflect blocks assigned to different observation stations.

#### Observations

Observations were made at all hours of the day from dawn to dusk and in all months of the year for three consecutive years. However, because not all of the observation area could be seen equally well before 0900 or after 1900 hours and because there were very few trout in the main observation area (A) from December through March, only data obtained between 0900 and 1900 hours April through November were included in statistical analyses. Once each hour, each brown trout in the observation area was located and identified ("scan" observations of Altmann 1974). Between these inventories each brown trout was observed in turn for 15 minutes (Altmann's "focal animal" observa-

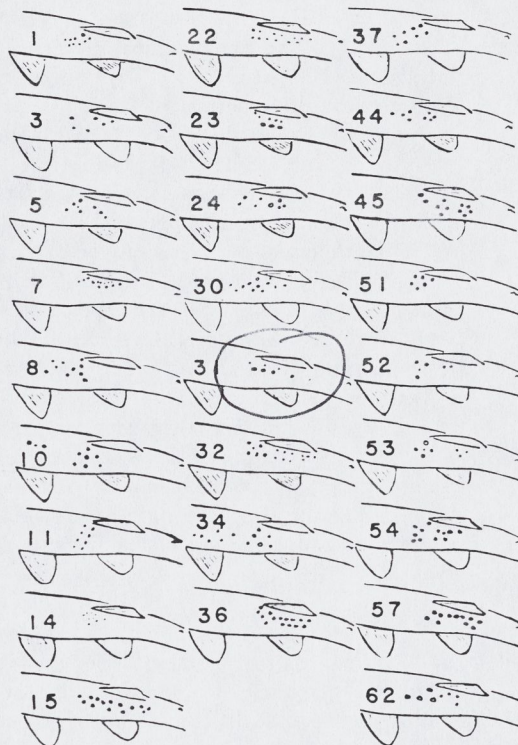


FIGURE 6.—Identifying spot patterns of 26 wild brown trout whose activity patterns were quantified in this study.

tions). If a particular fish was not in sight when its turn arrived, the next one on the numbered list was observed. By this system, the distribution of brown trout was mapped 10 times a day, and each individual was closely studied (on the average) every 2 days.

Feeding activity was categorized as surface, midwater, and bottom. A feed was recorded if a fish was seen to open its mouth, "chew," or swallow. If a brown trout's head broke the water surface during a feeding excursion, the fish had made a surface feed. If its head touched the bottom, this was a bottom feed. All others were recorded as midwater feeds: that is, the fish fed on organisms suspended in the water column.

The duration and frequency of "false rises," during which a fish rose from its holding position to inspect and reject an item in the drift, were determined from frame-by-frame analysis of videotape recordings.

Agonistic behavior was similar to that described by Kalleberg (1958), Keenleyside and Yamamoto (1962), Jenkins (1969), McLaren

Beehoven

(RISE FORM)  
← BOTTOM  
← "MID WATER"



(1979), and North (1979), and as recorded in the Encyclopedia Cinematographica film by Butler and Hawthorne (1975). The start, end, outcome, and location of each agonistic encounter was recorded, together with the identity of the fish involved. The winner was determined by the types of agonistic behavior displayed by each contestant.

Each time a brown trout moved to a different foraging site, the identification number of the site and the time the fish arrived at that site was recorded. Movement rates were later computed by dividing the number of times a fish moved to a new position during an observation period by the total time of the observation period.

The final type of activity recorded was a gape or yawn, characterized by an exaggerated extension of the opercula and upward rotation of the eyes not accompanied by any other movement.

#### *Data Recording*

Recording of observational data was greatly facilitated by the use of a microcomputer system designed specifically for this study. The system consisted of a power supply, KIM-1 programmable microprocessor, clock generator, program memory, random-access memory, and peripheral interface device (MOS Technology 1976). A keyboard allowed manual data input. At the start of each day the computer program was loaded from a cassette tape and the clock was synchronized with real time. Most data entries could be made with one or two keystrokes each because the computer automatically carried a fish's identity and its position in the observation area (entered at the start of each focal animal observation) through subsequent data entries until a new fish code or position code was recorded. Whenever an activity code was entered, the computer automatically recorded the fish's identity, position, and activity, together with date and time to the nearest 0.01 minute. Other codes recorded the start and end of agonistic encounters, the identity of the contestants, and the winner of each bout. Data were dumped to a cassette tape each evening. Later, the data were transferred for editing and processing to the Digital Equipment Corporation Model DEC-10 computer, operated by the Electrical Engineering Department of The Pennsylvania State University.

The activity of fish also was recorded at selected times on 16-mm motion-picture film and on videotape.

#### *Age and Length Determinations*

The age of young-of-the-year and yearling brown trout in Spruce Creek can readily be determined by size alone. The data of Beyerle and Cooper (1960) show no overlap in size between these two age groups in Spruce Creek and also show that most wild brown trout reach 200 mm total length by the end of their second year of growth (see also Fig. 2). Because young of the year in Spruce Creek emerge from the gravel over an extended period from late March through early May (Beyerle and Cooper 1960), March 1 was arbitrarily assigned the "birthday" of all wild fish.

New fish each year consisted of young of the year or yearlings only and many individuals were present throughout the course of the study. Consequently, the exact year class of most of the fish was known by the end of the study. The age of fish larger than 200 mm at the beginning of the study was conservatively estimated to be the minimum age at which fish of known age attained such length. The age of the largest fish, number 15, estimated at 6 in 1979 and 7 in 1980, was later confirmed by examination of the fish's otoliths (sagittae).

The length of individual fish (precision,  $\pm 5$  mm) was determined from photographs taken at known foraging sites. At the end of each season, after brown trout had left for spawning sites, photographs were taken of a metal rule in the exact position previously occupied by the fish. This technique eliminated all effects of parallax and refraction.

#### *Abiotic Variables*

Water temperature, turbidity, water-gage height, and light intensity were recorded for analysis of effect on brown trout behavior (Table 1). Water temperature was recorded continuously with Ryan recording thermographs. Turbidity, in standard nephelometric turbidity units, was measured daily with a Hach turbidimeter. Water height was measured daily with a stream gage installed throughout the duration of the study (Fig. 4). A measure of daily light intensity in arbitrary units was calculated from



the area under the curve of a Belfort recording pyrliometer.

#### *Hatchery Brown Trout*

On August 23, 1979, after the behavior of the resident population had been studied for approximately 2 years, 200 brown trout were obtained from the Big Spring hatchery in Cumberland County, Pennsylvania, and released in the study area. The hatchery fish were in their second year of growth and ranged from 28 to 35 cm in total length. The left pelvic fin was removed from each before release. They were observed as wild trout had been and those that took up residence were identified by spot patterns. For the first 4 days after the hatchery brown trout were stocked, the activities of both hatchery and wild fish were recorded simultaneously by two observers, who alternated observations between hatchery and wild fish.

To test for a difference in effect of stocking in spring versus late summer, 200 hatchery brown trout again were introduced on May 8, 1980. These, too, were obtained from the Big Spring hatchery and had the left pelvic fin removed, but they were smaller (23–30 cm) than those released the year before.

#### *Analysis*

##### *Statistical Analysis*

All statistical analyses were performed with Statistical Analysis System (SAS) computer programs (SAS Institute 1979).

Regression analyses of length and age were performed on data obtained from 218 photographs of 26 wild brown trout ranging from young of the year to age 8. Because some effect of repeated measures was unavoidable by this technique, confidence intervals reported may be underestimated. Rectangular-hyperbola and negative-exponential models were fitted by the Marquardt iterative method (Marquardt 1963).

Multiple-regression techniques were used to investigate various biotic and abiotic effects on seven behavioral rates: surface, midwater, bottom, and total feeding; agonistic interaction: gape; and movement. Abiotic variables included daily amount of solar incident radiation, water temperature, water turbidity, water height, and temporal effects. Temporal effects were broken down by year, month, and hour of day. Biotic

TABLE 1.—Range and means of abiotic variables for Spruce Creek used in analysis of variance of brown trout activity rates.

Variable	High	Low	Mean $\pm$ SD
Water temperature (C)	20.0	3.1	15.3 $\pm$ 2.5
Turbidity (nephelometric units)	7.5	2.5	4.2 $\pm$ 1.6
Water height (m)	0.22	0.15	0.19 $\pm$ 0.02
Light intensity (arbitrary units)	43 <sup>a</sup>	2 <sup>b</sup>	15.1 $\pm$ 9.4

<sup>a</sup> Cloudless day, midsummer.

<sup>b</sup> Rainy day, late fall.

effects considered were age, length, and dominance ranking of individual fish.

Exploratory analyses techniques revealed that season (month) was the most significant temporal variable and that the effect of year and hour could be ignored in subsequent analyses of variance.

Because the month effect was highly significant, but the interactions of month and the variables of interest were not, month was treated as an indicator variable (Neter and Wasserman 1974) in the formal testing of the effects of the independent biotic and abiotic variables. Any data transformations required to achieve normality are reported in context.

Not all individual fish were equally represented in the observation routine. The identity of all wild fish used in the analyses was known, so the most conservative inferences about the wild population were made by treating all wild individuals with equal weight, even though the total observation time differed from fish to fish. Activity rates were computed for each individual over the time period in question and each such rate was treated as a single datum.

##### *Time Budgets and Bioenergetic Costs*

The time it took wild brown trout to intercept food and to return to the site was determined by frame-by-frame analyses of videotape recordings with a videotape editor. Durations of gapes, agonistic encounters, and position changes were estimated by analysis of videotapes and cinematography. Relative bioenergetic costs of different activity states were estimated from tail-beat frequencies, determined similarly by analysis of videotapes and motion-picture sequences. The effect of fish size on tail-



TABLE 2.—Observations of brown trout in Spruce Creek: number of scans (quick inventories) during which a fish was sighted, and number of minutes a fish was observed during 15-minute studies of them (focal observations), 1978–1980.

Fish number	1978				1979				1980			
	Age	Rank	Focal minutes observed	Number of scans	Age	Rank	Focal minutes observed	Number of scans	Age	Rank	Focal minutes observed	Number of scans
1	3	5	354	44								
3					1	7	102	118	2	12	45	115
5	3	6	485	88	4	6	322	263				
7	4	1	350	63	5	5	221	105				
8	1	14	1,092	146	2	12	604	332	3	10	418	193
10	2	4	191	74	3	4	139	75	4	14	61	26
11	1	14	38	17	2	11	216	264	3	11	183	150
14	3	3	18	4	4	3	149	109	5	3	49	55
15	5	1	16	6	6	1	173	75	7	1	102	118
22	1	13	157	96								
23	2	12	431	111	3	8	205	198				
24	3	10	204	103	4	12	168	165				
30									1	15	102	108
31	2	9	1,501	145	3	9	466	254	4	9	576	184
32	2	11	1,041	131	3	11	554	310	4	11	166	69
34	2	13	747	128	3	10	414	301				
36									1	14	156	116
37									1	15	64	31
44	2	10	92	11	3	10	13		4		14	28
45	2	12	99	13								
51	4	2	51	9	5	2	126	145	6			
52	1	15	16	32	2	13	198	258				
53					1	14	289	231	2	14	205	166
54					1	15	125	121	2	13	124	109
57					1	13	131	114	2	12	181	153
62					1	13	109	75				
Hatchery					1		558		1		1,174	

beat frequency was small compared to the effects of activity states and was ignored.

#### Home Range

Home-range size was estimated from the areas of both the minimum convex polygon that enclosed 95% of the sightings of each fish (A1 index) and an ellipse based on the determinant of the covariance matrix of the sightings (A4 index of Jennrich and Turner 1969). The latter index is a parametric estimate of the area that accounts for 95% of the habitat used by each wild brown trout.

The utilization distribution (Jennrich and Turner 1969; Anderson 1982) of each wild brown trout, a nonparametric estimate of home range, was generated by a computer-mapping program called SYMAP (Dougenik and Sheehan 1975). This program creates a contour map by interpolating a continuous surface in the region where there are no data points. A three-

dimensional visual representation of the utilization distribution was created by a computer-graphics program SYMVU (LCGSA 1977).

#### Behavior of Wild and Hatchery Fish

Because not all hatchery brown trout had been individually identified at the start of the comparative study, activities were analyzed on the basis of observation periods rather than individual fish. This resulted in a certain amount of repeated measures, but was unavoidable. Consequently, confidence intervals reported for comparative behavior of hatchery and wild trout may be underestimated.

The data were partitioned into two separate distributions for analysis: (1) rates, given that the activity did occur during an observation (zero rates were dropped from the analyses); and (2) proportions of observations in which an activity did or did not occur. The former distributions then were tested for normality; if an appropri-



ate transformation achieved normality, a *t*-statistic was calculated to test the hypothesis that the means of two groups of data are unequal.

The difference in proportions of non-zero observations between hatchery and wild activity was tested with the  $(1 - \alpha)$  confidence interval for the difference between the proportions of a binomial distribution (Walpole and Myers 1972;  $\alpha$  is the probability of a type-I error, and  $[1 - \alpha]$  is converted to percent).

### Results

Of the 18 wild brown trout resident in observation area A in 1978, 15 were present again in 1979. Twelve of the 20 fish observed in 1979 returned again in 1980 (Table 2). Both in 1979 and 1980, all new fish were young of the year or yearlings. Even though it was suspected that two or three older fish were removed by poachers early in the spring of 1980 (fish 51 had been positively identified in March) no age-group 2 or older brown trout moved in to take their places.

#### Home Range

The mean home-range size of 53 wild brown trout was  $15.6 \text{ m}^2$  (SE, 1.7) as determined from minimum-convex polygons encompassing 95% of the scan sightings of each fish each year. The home-range size decreased steadily during the second through fifth years of growth (age groups 1–4) (Spearman's rank correlation coefficient  $r = -0.34$ ;  $P = 0.02$ ;  $N = 47$ ) but then increased (Fig. 7). Home-range estimates based on the bivariate normal assumptions of Jennrich and Turner (1969) also yielded a negative but nonsignificant correlation (Spearman's  $r = -0.15$ ;  $P = 0.31$ ) for age groups 1–4, and an overall mean area of  $47.7 \text{ m}^2$ , three times that obtained by the polygon technique.

Each wild brown trout used only a portion of the total  $182\text{-m}^2$  observation area and remained faithful to the same part of the area from year to year (Fig. 8). No fish had exclusive use of any home range; considerable overlap existed in the home ranges of neighboring wild brown trout. For example, in 1979 the home range of fish 31 was wholly contained within that of fish 10, site 18 being the most frequently used foraging site by both fish (Fig. 9). None of the 20 wild brown trout resident in area A in 1979 was ever seen in area B despite over 100 hours of obser-

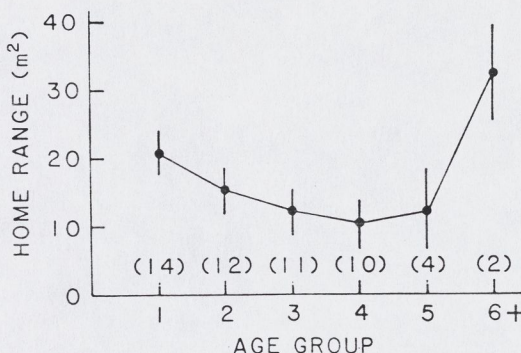


FIGURE 7.—Mean size ( $\pm$ SE) of home ranges for six age groups of wild brown trout as determined by the minimum-convex-polygon method. Sample sizes are in parentheses.

vation from tower 4. Neither was any of the eight brown trout resident in area B ever seen in area A, although area B was less than 30 m upstream and in the same pool as area A (Figs. 2 and 3). This is further confirmation of the small home ranges used by wild brown trout in Spruce Creek.

#### Foraging and Refuge Sites

Within their home range, individual wild brown trout used from 1 to 32 foraging sites, the mean number accounting for 90% of focal animal observations being  $6.0 \pm 0.5$  (SE;  $N = 52$  fish). From these sites, the fish darted to intercept food items in the drift and to pick up organisms attached to or moving about on the substrate.

Typically, foraging sites were in front of a submerged rock, or on top of but on the downward-sloping rear surface of a rock (Fig. 10). From there the fish had an unobstructed view of oncoming drift. While a wild brown trout was in such a site, its tail beat was minimal (see page 23), indicating that little effort was required to maintain a stationary position even though the current only millimeters overhead was as high as 60 to 70 cm/second. Most brown trout could be found in one of several such sites day after day (Fig. 10), and it was not uncommon to find a fish using many of the same sites for three consecutive years (Fig. 11).

The precision with which brown trout used foraging sites gives an indication of the latter's function and importance. The position of the



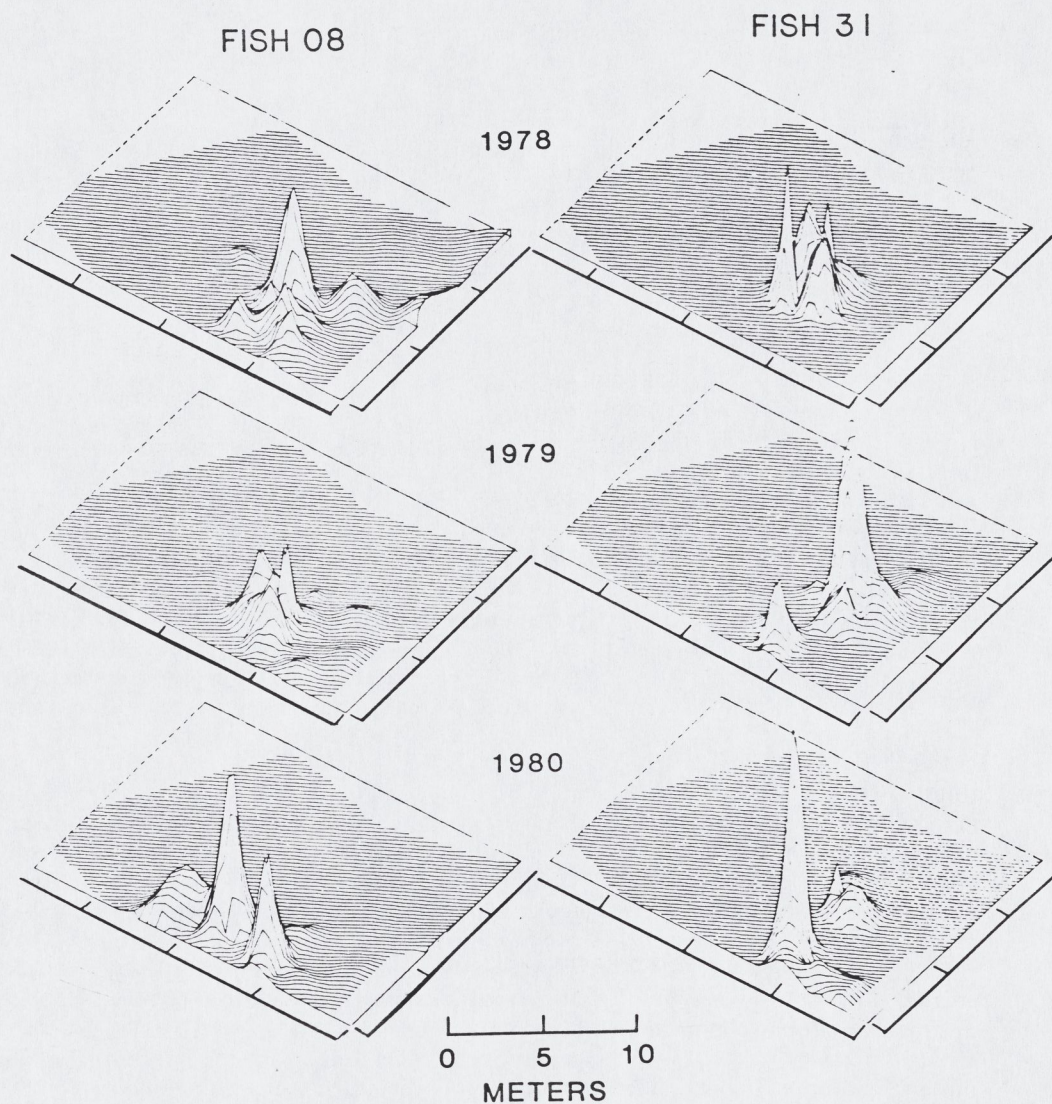


FIGURE 8.—Utilization distributions for wild brown trout 8 (year class 1977) and wild brown trout 31 (year class 1976) in 1978, 1979, and 1980. Shaded area represents observation area A. Peaks represent percent of time the fish was observed in specific foraging sites.

eye of fish 31 in position 18 (Fig. 10) in eleven photographs taken over 15 months ranged less than 40 mm in a longitudinal stream direction (SD, 11.7 mm), and cross-stream range was less than half of that. The position of the eye of fish 32 in the three photographs of Fig. 11 is virtually identical. This precision, together with the ease with which the wild brown trout were able to maintain these positions, demonstrates the cost-minimizing utility of the sites.

Many sites were used by more than one brown trout during a day (Fig. 9). Different fish used a particular site in the same way and with the same precision. Even though some smaller rocks shifted and moved during the course of the study, the foraging sites, created by the unique flow of water over and around the larger embedded rock, remained fixed. The most distinctive characteristic of the foraging sites was the low water velocity (about 8 cm/second) in



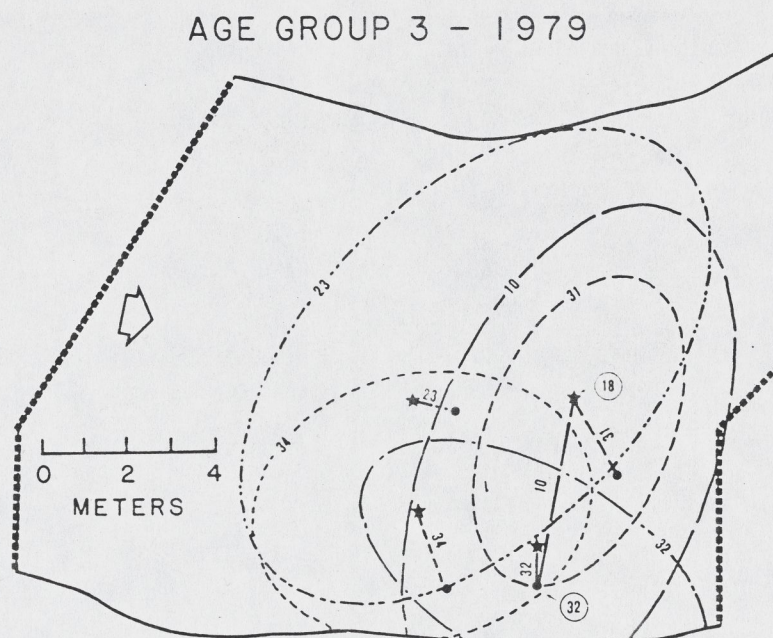


FIGURE 9.—Home ranges of five age-3 wild brown trout in 1979, as estimated by the Jennrich and Turner (1969) method. Site 18 was the primary (most often used) site for both fishes 10 and 31 and site 32 was the secondary site for both fishes 10 and 32 that year. Primary sites are indicated by stars, secondary sites by dots.

the immediate vicinity of the resident brown trout's head (Pierce 1982).

The precision with which brown trout used foraging sites precluded there being more than one fish at a site at a time. The distance between adjacent occupied foraging sites was rarely less than 1.5 m and if two brown trout were feeding within sight of each other, the larger of the two was always upstream.

Refuge sites were those sites to which trout fled when disturbed. Because wild brown trout rarely used refuge sites and because the experimental design of the study precluded observation of some fish in refuge sites, comments concerning these sites must be considered anecdotal.

The overhead flight of a large bird such as a mallard *Anas platyrhynchos* or common grackle *Quiscalus quiscula* typically caused a wild brown trout to dart to one side or another and become motionless with its body pressed tightly to the substrate. With no further stimulus, the fish would usually return to its foraging site and resume feeding within 3 to 5 minutes. Repeated alarm stimulus or stronger initial stimulus (such as a mallard landing) would cause the fish to

flee to deep water and become motionless or to move under a bank, rock, or some brush. In such a case, the fish would usually return to a foraging site in about 20 to 30 minutes.

Typically, more than one wild brown trout fled to the same pocket of deep water or under the same bank, rock, or brush. On one occasion a 2-year-old brown trout was observed tucked tightly along and partly under the down-stream side of a flat rock, perpendicular to the flow of the stream. It remained there for about 2 hours without any movement. It suddenly left this position, proceeded to one of its accustomed foraging sites, and started feeding. Other brown trout were occasionally seen lying motionless under brush (sometimes only the tip of the tail could be seen). Fish in refuge sites did not feed, did not move, and engaged in no agonistic encounters.

#### *Feeding, Position Change, and Gaping*

The mean total feeding rate, averaged over all months from April through November, steadily declined with increasing age from 20.2 feeds per 15 minutes for age-group 1 to 5.6 feeds per 15 minutes for age-group 6+ (Fig. 12;





FIGURE 10.—Wild brown trout 31 in site 18 on successive days during summer 1979.

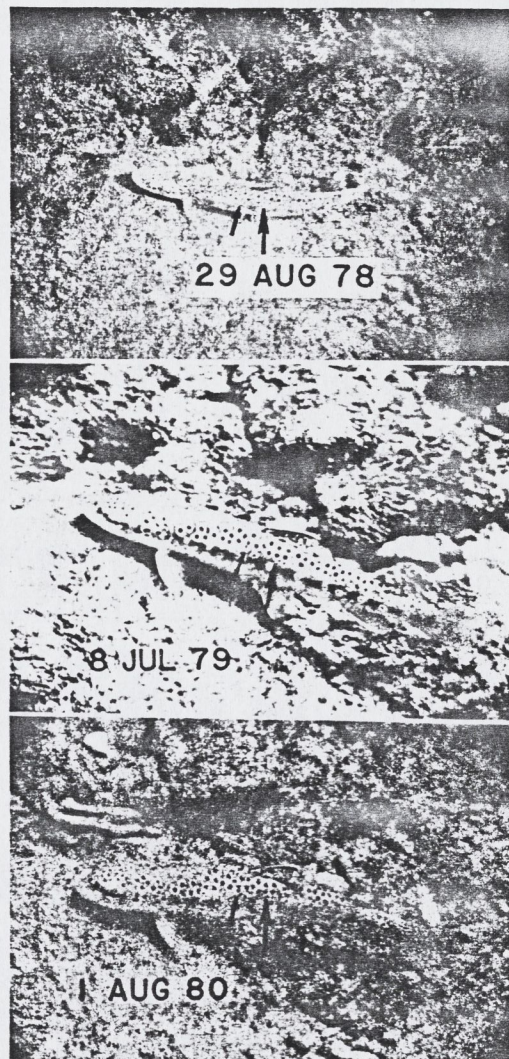


FIGURE 11.—Wild brown trout 32 in site 2 in three successive summers. The rectangular group of six spots below the dorsal fin (large arrow) and the two small spots close together (small arrow) were key identifying features.

Tables 3 and 4). The proportion of surface and midwater feeds was approximately the same for all age groups; bottom feeds accounted for only 7-13% of the total. On numerous occasions, small fish fed close to, but downstream from, a larger, more dominant fish, and at a higher rate than the upstream dominant. The larger fish

was passing up some items in the drift that the smaller wild brown trout ate.

Feeding rates were highest in spring, declined in July and August, and then increased again in September and October. Surface and midwater rates were about equal April through August but surface feeding was predominant in fall. Mean bottom-feeding rate was low throughout the year (Table 3).

Total feeding rates were higher on days when



- - SURFACE (DISTINCT RISE FORM)  
 △ - No rise form  
 □ - Head touched bottom when it fed.

#### FORAGING BEHAVIOR OF FREE-RANGING BROWN TROUT

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older fish were seen in observation area A. The mean feeding rate (feeds per 15 minutes) of young fish (age groups 1-4) on days when age groups 5 and older were seen in daily scan observations was  $20.4 \pm 2.1$  (SE;  $N = 49$ ), and it was only  $15.4 \pm 0.8$  ( $N = 67$ ) when older fish were not seen ( $F = 6.40$ ;  $P = 0.013$ ).

Total and midwater feeding rates were significantly higher on sunny days than on cloudy days. Increase in water temperature appeared to have a depressing effect on midwater and total feeding rates, even when corrected for the effect of month (Table 4). The only significant effect of turbidity was a depressing effect on bottom-feeding rates.

The number of times a fish moved from one foraging site to another during a 15-minute observation was highest in April and May and declined steadily throughout the rest of the year (Table 3). Neither size nor age had a significant effect on movement rate of the younger fish (<4 years old) but larger fish (older than age 3) moved less than younger fish (Tables 3 and 4). The time of day had no significant effect on the movement rates of the fish (Table 3), nor did any of the abiotic variables measured: turbidity; light intensity; water temperature; water height (Table 4).

There was a very pronounced temporal effect on the rate at which the fish gaped, which was highest during summer months and lowest during the middle of the day (Fig. 13). When corrected for the confounding effect of month, gape rate was highly correlated with water temperature, but turbidity had no significant effect (Table 4). No difference in the frequency of gaping was evident among the various age groups.

#### Growth

Growth of brown trout was curvilinear with age; a rectangular hyperbola fit the data better than a negative exponential, which gave too low an asymptotic length (Table 5, Fig. 14). For the rectangular hyperbola, parameter estimates did not differ between the model of all fish and of the subset of fish aged 0-4 (regression analysis;  $P \leq 0.05$ ), indicating that the lengths of older fish could be predicted by the growth of younger age groups.

Growth of older brown trout in the study area was very slow. This is exemplified by fish 15, dominant in the area during 1978, 1979, and

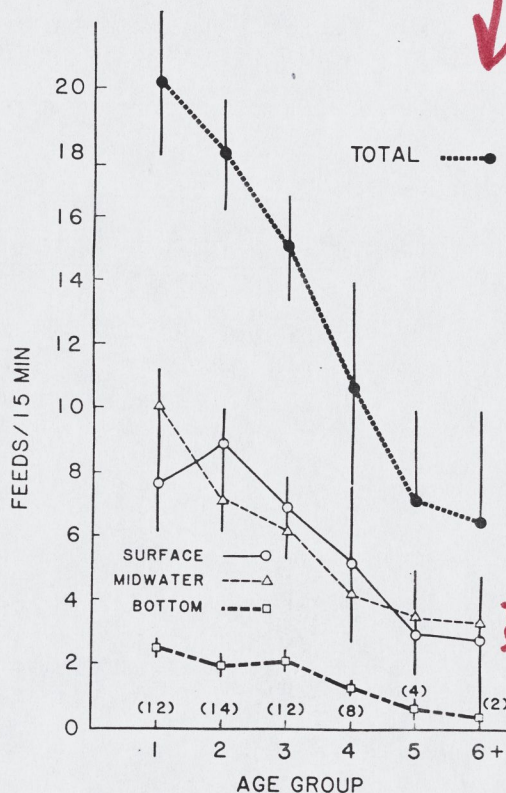


FIGURE 12.—Mean ( $\pm$ SE) feeding rates for six age groups of wild brown trout: total rates and rates for surface, midwater, and bottom feeding. Number of fish in each age group is in parentheses.

1980. In August 1977, it was 28.3 cm long and it grew slightly less than 4 cm over the next 4 years. Scale samples taken from this fish in October 1981 yielded only one unregenerated scale out of 78 taken, and that scale contained only three distinct annuli. Fish 15 was captured and killed in April 1982. The otoliths (sagittae) displayed 9 distinct annuli, confirming the age estimates used for this fish throughout the study.

#### Dominance Hierarchy

Dominance hierarchies of wild brown trout in observations area A were nearly linear and quite consistent from year to year (Fig. 15, Tables 6-8). Fish 15, never observed to lose an agonistic encounter in 3 years, ranked first. Other wild brown trout were ranked 2-15, based on the number of fish in the longest linear chain, which occurred in 1979. Dominance was strongly correlated with age (Spearman's  $r =$

NOT STATISTICALLY DIFFERENT  
 Essentially the same proportion regardless of age (size) of fish.



TABLE 3.—Activities of wild brown trout in observation area A of Spruce Creek, stratified by age group, time of day, and season. Within a stratum, means with a letter in common are not significantly different (Duncan's multiple-range test;  $P > 0.05$ ).

Age, hour or month	Number of fish	Mean number per 15 minutes $\pm$ SE								Number of focal observations
		Agonistic encounters	Feeds					Moves	Gapes	
			Surface	Midwater	Bottom	Total				
Age										
1	12	2.1 $\pm$ 0.5 a	7.6 $\pm$ 1.6 ab	10.0 $\pm$ 1.2 a	2.6 $\pm$ 0.3 a	20.2 $\pm$ 2.2 a	2.6 $\pm$ 0.6 a	1.08 $\pm$ 0.16 a	168	
2	14	1.8 $\pm$ 0.2 a	8.9 $\pm$ 1.0 a	7.1 $\pm$ 1.0 ab	1.9 $\pm$ 0.2 ab	18.0 $\pm$ 1.7 a	2.5 $\pm$ 0.5 a	0.79 $\pm$ 0.10 a	350	
3	12	1.9 $\pm$ 0.3 a	6.9 $\pm$ 1.0 ab	6.1 $\pm$ 0.8 b	2.1 $\pm$ 0.4 ab	15.1 $\pm$ 1.7 ab	2.9 $\pm$ 0.7 a	0.75 $\pm$ 0.15 a	252	
4	8	1.7 $\pm$ 0.2 a	5.2 $\pm$ 2.5 ab	4.2 $\pm$ 1.0 b	1.3 $\pm$ 0.2 bc	10.8 $\pm$ 3.2 ab	1.2 $\pm$ 0.6 a	0.85 $\pm$ 0.14 a	133	
5	4	2.0 $\pm$ 0.2 a	2.9 $\pm$ 1.2 b	3.5 $\pm$ 1.4 b	0.6 $\pm$ 0.2 cd	7.1 $\pm$ 2.8 b	2.7 $\pm$ 0.4 a	0.86 $\pm$ 0.40 a	38	
6+	2	0.8 $\pm$ 0.1 b	2.8 $\pm$ 2.6 ab	3.3 $\pm$ 1.3 b	0.4 $\pm$ 0.1 cd	6.6 $\pm$ 3.6 b	1.1 $\pm$ 0.6 a	0.34 $\pm$ 0.31 a	21	
Hour of the day <sup>a</sup>										
0900	27	0.9 $\pm$ 0.2	6.7 $\pm$ 1.7	5.3 $\pm$ 0.9	1.9 $\pm$ 0.4	13.8 $\pm$ 2.2	2.0 $\pm$ 0.3	1.05 $\pm$ 0.10	105	
1000	33	1.1 $\pm$ 0.2	5.3 $\pm$ 1.0	5.6 $\pm$ 0.7	2.0 $\pm$ 0.5	12.8 $\pm$ 1.5	2.7 $\pm$ 0.4	1.19 $\pm$ 0.16	105	
1100	30	1.5 $\pm$ 0.3	6.2 $\pm$ 0.9	5.4 $\pm$ 0.7	1.6 $\pm$ 0.3	13.2 $\pm$ 1.4	3.6 $\pm$ 0.5	0.94 $\pm$ 0.10	113	
1200	26	1.0 $\pm$ 0.2	6.3 $\pm$ 1.1	5.7 $\pm$ 0.7	2.2 $\pm$ 0.4	14.3 $\pm$ 1.3	2.7 $\pm$ 0.1	0.70 $\pm$ 0.10	98	
1300	27	1.4 $\pm$ 0.2	5.5 $\pm$ 1.0	6.9 $\pm$ 1.4	1.6 $\pm$ 0.3	13.9 $\pm$ 2.1	3.3 $\pm$ 0.4	0.60 $\pm$ 0.10	135	
1400	30	1.2 $\pm$ 0.2	8.2 $\pm$ 2.4	7.0 $\pm$ 1.1	1.9 $\pm$ 0.4	17.1 $\pm$ 2.5	3.0 $\pm$ 0.5	0.63 $\pm$ 0.08	117	
1500	30	1.4 $\pm$ 0.2	6.3 $\pm$ 1.4	8.1 $\pm$ 1.5	1.9 $\pm$ 0.3	16.3 $\pm$ 2.1	2.9 $\pm$ 0.4	0.95 $\pm$ 0.17	95	
1600	33	1.3 $\pm$ 0.2	4.2 $\pm$ 0.8	7.4 $\pm$ 1.8	1.3 $\pm$ 0.3	12.9 $\pm$ 2.6	2.4 $\pm$ 0.4	1.00 $\pm$ 0.12	104	
1700	22	1.1 $\pm$ 0.2	7.2 $\pm$ 1.8	6.3 $\pm$ 1.3	1.8 $\pm$ 0.4	15.3 $\pm$ 2.6	1.7 $\pm$ 0.3	0.96 $\pm$ 0.12	61	
1800	10	1.0 $\pm$ 0.5	5.3 $\pm$ 1.4	6.1 $\pm$ 1.5	1.3 $\pm$ 0.5	12.7 $\pm$ 2.7	1.8 $\pm$ 0.5	0.97 $\pm$ 0.23	14	
Month										
Apr	9	0.9 $\pm$ 0.3 cd	8.6 $\pm$ 2.4 ab	8.6 $\pm$ 1.7 a	6.0 $\pm$ 2.3 a	23.2 $\pm$ 3.0 a	4.4 $\pm$ 1.6 ab	0.04 $\pm$ 0.04 d	21	
May	22	1.7 $\pm$ 0.4 ab	8.3 $\pm$ 1.8 a	9.9 $\pm$ 0.7 a	2.9 $\pm$ 0.6 a	21.1 $\pm$ 2.0 a	4.3 $\pm$ 0.5 a	0.72 $\pm$ 0.11 ab	125	
Jun	20	1.9 $\pm$ 0.3 a	9.6 $\pm$ 2.1 a	10.9 $\pm$ 2.5 a	2.5 $\pm$ 0.7 a	23.0 $\pm$ 3.7 a	3.6 $\pm$ 0.3 ab	0.90 $\pm$ 0.12 ab	166	
Jul	27	0.9 $\pm$ 0.1 bc	7.2 $\pm$ 1.0 ab	7.9 $\pm$ 1.1 a	1.7 $\pm$ 0.2 a	16.8 $\pm$ 1.7 ab	2.8 $\pm$ 0.2 b	1.07 $\pm$ 0.15 a	261	
Aug	30	1.0 $\pm$ 0.2 cd	3.8 $\pm$ 0.7 bc	3.7 $\pm$ 0.6 b	1.6 $\pm$ 0.2 a	9.1 $\pm$ 1.2 d	2.1 $\pm$ 0.2 bc	0.87 $\pm$ 0.13 a	329	
Sep	12	1.2 $\pm$ 0.7 cd	9.2 $\pm$ 2.5 ab	2.8 $\pm$ 0.6 b	0.5 $\pm$ 0.2 b	12.5 $\pm$ 2.7 cd	1.3 $\pm$ 0.4 cd	0.54 $\pm$ 0.24 bc	30	
Oct	10	0.7 $\pm$ 0.2 cd	12.1 $\pm$ 3.2 a	2.6 $\pm$ 0.3 b	0.7 $\pm$ 0.2 b	15.4 $\pm$ 3.4 bc	1.0 $\pm$ 0.4 cd	0.07 $\pm$ 0.05 d	20	
Nov	7	0.3 $\pm$ 0.2 d	1.1 $\pm$ 0.4 c	0.5 $\pm$ 0.2 c	0.7 $\pm$ 0.2 b	2.3 $\pm$ 0.8 e	0.8 $\pm$ 0.3 cd	0.16 $\pm$ 0.08 cd	22	

<sup>a</sup> No significant effect of time of day on any activity.

0.81;  $P = 0.01$ ;  $N = 50$ ), although the agonistic encounter rate was essentially the same for age groups 1 through 5 (Table 3). There was no significant effect of dominance on any of the seven behaviors tested (Table 4). Agonistic encounter rates were highest in May and June, corresponding to the months of highest feeding rates (Table 3), but time of day had no significant effect on agonistic behavior. Of the four abiotic variables measured, only water height had a significant (positive) effect on agonistic behavior (Table 4).

#### Use of Cover

One of the most surprising results of this study was the high probability of sighting an individual wild brown trout in a foraging site during scan and focal-animal observations. Age-2 wild brown trout were found during 83% of the scans between 0900 and 1900 hours. If one defines

"cover" as concealment from above, age-2 brown trout spent less than 17% of those hours under cover. As the fish got older, they were less likely to be seen (Fig. 16). Because part of the home range of some fish was not wholly within the observation area and the cryptic coloration of the fish inevitably results in some fish being missed in a scan observation, the data in Fig. 16 must be considered very conservative estimates of the time the fish were not under overhead cover. The overall mean probability of sighting an individual of any age group (given that it was seen at least once that day) ranged from a low of  $0.64 \pm 0.07$  (SE) in April and May to  $0.81 \pm 0.02$  in November.

#### Time and Energy Budgets

It took brown trout only 1 second to intercept food items in the drift or capture organisms on the bottom from their stationary foraging sites,



TABLE 4.—Relationships of activity rates (events / 15 minutes) of wild brown trout in Spruce Creek with fish age, length, dominance rank, and abiotic variables, corrected for effect of month. Asterisks (\*) indicate significant slopes ( $P \leq 0.05$ ). Abbreviations:  $b$  = slope;  $P$  = probability;  $N$  = number of observations; Trans = transformation of dependent variable (CBRT = cube root;  $1/X$  = inverse of dependent variable; SQRT = square root).

Independent variable	Agonistic encounters	Feeds				Gapes	Moves
		Surface	Midwater	Bottom	Total		
Age							
<i>b</i>	-0.0009	-0.0275*	-0.0219*	+0.0048*	-0.1787*	+0.0006	-0.0100*
<i>P</i>	0.3766	0.0003	0.0001	0.0001	0.0001	0.4510	0.0006
<i>N</i>	137	170	152	152	183	132	152
Trans	1/ <i>X</i>	CBRT	Log <sub>e</sub>	1/ <i>X</i>	SQRT	1/ <i>X</i>	Log <sub>e</sub>
Length							
<i>b</i>	-0.0044	-0.0366*	-0.0640*	+0.0125*	-0.1415*	+0.0016	-0.0278*
<i>P</i>	0.2272	0.0005	0.0001	0.0001	0.0001	0.5430	0.0051
<i>N</i>	137	171	152	152	185	132	152
Trans	1/ <i>X</i>	CBRT	Log <sub>e</sub>	1/ <i>X</i>	SQRT	1/ <i>X</i>	Log <sub>e</sub>
Dominance							
<i>b</i>	-0.0044	-0.0517	+0.0104	-0.0039	-0.0355	+0.0024	+0.0338
<i>P</i>	0.6004	0.0530	0.4926	0.4637	0.4881	0.7007	0.1716
<i>N</i>	48	46	50	50	51	47	50
Trans	1/ <i>X</i>	CBRT	Log <sub>e</sub>	1/ <i>X</i>	SQRT	1/ <i>X</i>	Log <sub>e</sub>
Turbidity							
<i>b</i>	-0.0013	-0.0237	-0.0732	+0.0431*	-0.1690	+0.0019	-0.0597
<i>P</i>	0.3114	0.6727	0.1624	0.0002	0.0847	0.8550	0.3244
<i>N</i>	173	153	173	126	186	109	145
Trans	1/ <i>X</i>	Log <sub>e</sub>	Log <sub>e</sub>	1/ <i>X</i>	SQRT	1/ <i>X</i>	Log <sub>e</sub>
Light intensity							
<i>b</i>	-0.0009	+0.0097	+0.0097*	+0.0019	+0.0077*	+0.0003	-0.0015
<i>P</i>	0.4598	0.1119	0.0351	0.0633	0.0374	0.6974	0.8112
<i>N</i>	171	250	279	211	293	175	224
Trans	1/ <i>X</i>	Log <sub>e</sub>	Log <sub>e</sub>	1/ <i>X</i>	SQRT	1/ <i>X</i>	Log <sub>e</sub>
Water temperature							
<i>b</i>	-0.0031	+0.0231	-0.0543*	+0.0083	-0.0642*	-0.0179*	+0.0567
<i>P</i>	0.7279	0.5055	0.0385	0.1775	0.0016	0.0020	0.1607
<i>N</i>	252	371	417	339	401	290	299
Trans	1/ <i>X</i>	Log <sub>e</sub>	Log <sub>e</sub>	1/ <i>X</i>	SQRT	1/ <i>X</i>	Log <sub>e</sub>
Water height							
<i>b</i>	-0.6932*	-1.1846	+1.3345	-0.1789	+3.0000	-0.2479	-0.5911
<i>P</i>	0.0099	0.3056	0.1806	0.4517	0.1112	0.1781	0.5709
<i>N</i>	136	193	217	160	230	135	176
Trans	1/ <i>X</i>	Log <sub>e</sub>	Log <sub>e</sub>	1/ <i>X</i>	SQRT	1/ <i>X</i>	Log <sub>e</sub>

but because the current swept the fish farther downstream during a surface feed it took the fish longer (6 seconds) to return to the site after a surface feed than for either a midwater or bottom feed (Table 9). A rough approximation of the comparative energetic cost of the several activities may be obtained from the tail-beat frequencies of the trout in different activity states (Table 10). The high energetic cost of surface feeding is evident from the relative duration of, and tail-beat frequency during, surface feeding. Stationary swimming at the surface, an even more costly activity, was very rare (much less

than 1% of observations) and always was associated with very high feeding rates (30–40 feeds/15 minutes). The percent of time spent in each behavioral state for each age group was calculated from the general equation:

$$\% \text{ activity} = 100(\text{mean duration of activity} \times \text{mean activity rate}) / \text{observation time}.$$

The wild brown trout in Spruce Creek spent less than 14% of their foraging time in energetically costly activity (Table 11). They spent most of their daylight time, an average of 86%, in a sit-and-wait state, searching the passing



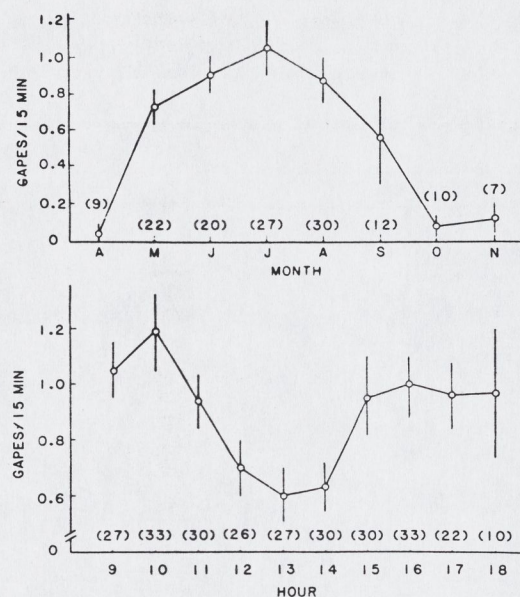


FIGURE 13.—Mean ( $\pm$ SE) gape rates of wild brown trout for April through November and 0900–1900 hours averaged over 3 years (1978–1980). Number of fish is in parentheses.

water column for drifting food. The cost-saving value of such behavior is evident from the low tail-beat frequencies and time spent in such states. As the fish got older, a greater proportion of time was spent in agonistic encounters and a smaller proportion in pursuit of food. Overall, the fish became less active as they got older (Table 11).

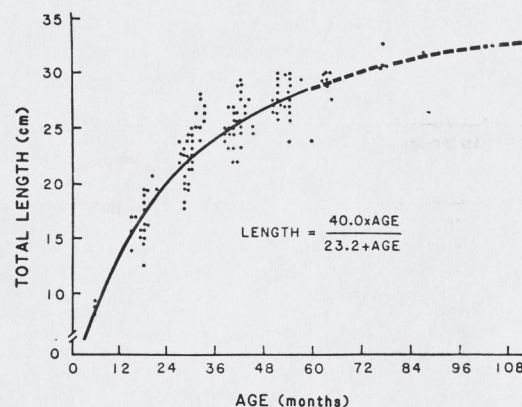


FIGURE 14.—Length-age relationship for wild brown trout in Spruce Creek. Dots are empirical; the rectangular hyperbola was fitted to them by least-squares. Broken portion of curve reflects minimum age estimates of trout older than 4+.

#### Hatchery Brown Trout

Within 20 minutes after the hatchery fish were introduced, the wild brown trout engaged the hatchery fish in agonistic encounters. Most agons were started by the wild fish but there was no prior residence effect in the outcome of encounters between wild and hatchery fish. Of 197 contests, 83 were won by wild fish and 96 were won by hatchery fish (Tables 7 and 8). There was, however, a significant correlation between the dominance rank of the wild fish (as determined from agonistic encounters among wild fish) and the proportion of agonistic encounters between wild and hatchery fish that a

TABLE 5.—Growth models for brown trout in Spruce Creek, fit by nonlinear regression.  $L_{max}$  and  $L_0$  are asymptotic total lengths for rectangular-hyperbola and exponential models, respectively.  $A_{1/2}$  is age at which half of asymptotic length is attained;  $B_1$  is exponential time constant.

Model	N	Sum of squares	Parameter		
			Symbol	Estimate	Asymptotic 95% confidence interval
Rectangular hyperbola <sup>a</sup>	218	Regression, 128,333.6	$L_{max}$	40.0 cm	38.4, 41.6
		Residual, 643.8	$A_{1/2}$	23.2 months	20.7, 25.7
Rectangular hyperbola <sup>a</sup> (ages 0–4 only)	154	Regression, 76,897.6	$L_{max}$	40.3 cm	37.0, 43.6
		Residual, 539.3	$A_{1/2}$	23.6 months	19.1, 28.0
Negative exponential <sup>b</sup>	218	Regression, 128,316.9	$L_0$	30.8 cm	30.0, 31.6
		Residual, 660.4	$B_1$	0.045	0.041, 0.047

<sup>a</sup> Rectangular hyperbola model:  $L = L_{max}Age / (A_{1/2} + Age)$ .

<sup>b</sup> Negative exponential model:  $L = L_0[1 - \exp(-B_1Age)]$ .



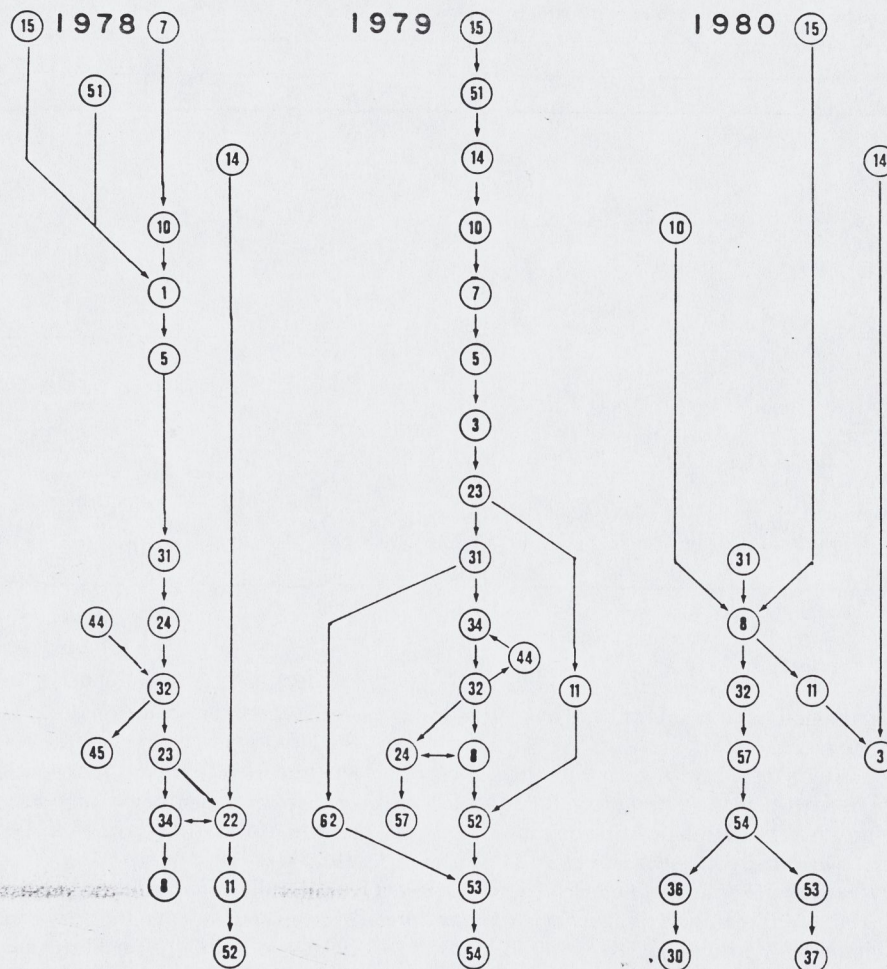


FIGURE 15.—Social hierarchies of wild brown trout resident in observation area A, 1978–1980, based on outcomes of agonistic encounters. Highest rank is at top. Number in circle is the fish identification number.

wild fish won ( $r = -0.37$ ;  $P = 0.03$ ;  $N = 32$ , Spearman's rank correlation coefficient). The large, high-ranking wild fish repeatedly chased the hatchery fish completely out of the observation area. Fish 15, the oldest wild brown trout in observation area A, never lost an agonistic encounter with any brown trout, wild or hatchery, during the observation periods 1978 through 1980 (Tables 6–8). Although agonistic encounters between wild brown trout rarely exceeded 30 seconds, those between wild and hatchery trout were frequently very prolonged. On one occasion wild fish 31 engaged seven hatchery fish in a series of agonistic bouts that

lasted 3.5 minutes. At the end of this series, fish 31 was breathing heavily, had a dark, blotchy color, and appeared exhausted. Other wild brown trout similarly exhibited evidence of stress, not seen before the introduction of hatchery fish.

A few hatchery brown trout took up stationary positions in foraging sites used by wild brown trout. Some hatchery trout were observed in these discrete sites only minutes after they were stocked and before they had started to feed. They used these common sites with a precision similar to that of the wild brown trout. A few hatchery brown trout displaced wild fish from



TABLE 6.—Outcomes of agonistic encounters between brown trout (identified by number), 1978.

Winning fish	Losing fish																		Total wins
	1	5	7	8	10	11	14	15	22	23	24	31	32	34	44	45	51	52	
1	—	2								1		1	2	2	2	1			11
5		—		2	1					1		8	4	3		2			21
7	2	3	—	4	3					1	4	3	1	5					26
8	1			—										2					3
10	1			3	—	4				1		10	4	1				3	27
11						—													0
14							—		3									1	4
15	1							—						1					2
22						1			—			1		1					3
23				2		1			1	—				4					8
24										1	—		2						3
31		3		46	3				8	7	1	—	16	11		1		3	99
32		1		19	1					1		2	—	7	1	8			40
34				5					1	1	1			—					8
44				2									6		—	1			9
45																—			0
51	1									1				1			—	1	4
52																		—	0
Total losses	5	10	0	83	8	6	0	0	13	15	6	25	35	38	3	13	0	8	268

these preferred foraging sites and even appeared to become integrated into the dominance hierarchy of the wild fish for short periods. Unlike the wild brown trout, however, the hatchery brown trout often failed to return to the site after an agonistic encounter or after they had pursued food items in the drift.

Most hatchery fish moved almost constantly, or remained stationary in other, less energy-saving sites. The tail-beat frequency in such cases was significantly higher than that of hatchery or wild fish using numbered sites. The overall mean tail-beat frequency for stationary hatchery fish was  $1.93 \pm 0.10$  (SE) beats/second ( $N = 34$ ) as compared to  $0.43 \pm 0.03$  beats/second ( $N = 45$ ) for stationary wild fish. The tail-beat frequency of moving hatchery fish,  $2.31 \pm 0.12$  beats/second ( $N = 16$ ) was similar to that of moving wild fish (Table 10).

The hatchery brown trout fed less, and changed position more frequently, than wild fish in both 1979 and 1980 (Table 12). Gape rates were similar for both types of brown trout.

The number of hatchery brown trout declined continuously after they were stocked in observation pools in 1979 and 1980 (Fig. 17). The decline was more rapid in 1979 (when wild trout also decreased in abundance) than it was in 1980. Only 2 of the 179 hatchery fish stocked in the observation pool in 1979 were seen again

in 1980. When seen (once, in early April) they were thin and moving almost continuously. Very few, if any, of the brown trout stocked in 1980 wintered over. In October 1981, when the entire area was censused by electrofishing, none of the 400 hatchery fish stocked in 1979 and 1980 was recovered.

Overall, the behavior of the smaller hatchery brown trout stocked in the spring of 1980 more nearly resembled that of the wild fish than did the behavior of larger fish stocked in late summer 1979.

#### Discussion

The foraging behavior of wild brown trout in Spruce Creek reflects the profound effect that current has on the energy fish must expend while living in a lotic environment. The restricted home range of individual fish, the discrete nature of the foraging sites within these home ranges, and the large proportion of time the fish spend stationary in foraging sites suggest that energy expended by the wild brown trout may be a principal determinant of growth rate and population density in Spruce Creek.

#### Home Range

The restricted nature of the home range of stream-living trout and juvenile salmon has been inferred by many investigators (Stefanich 1952;



Holton 1953; Miller 1954a, 1957; Newman 1956; Saunders and Gee 1964; Edmundson et al. 1968; Bohlin 1977), but the present study may be the first in which the actual home-range size of free-ranging salmonids has been measured by direct observation. Schuck (1945) reported that most wild brown trout in Crystal Creek, New York, were recaptured by electro-fishing in the same sections of stream where they had been originally captured and tagged. He also noted a homing tendency. Many fish caught in an upstream weir during the spawning run later were recaptured in the same section where they had been originally captured, tagged, and released. Miller (1954a) reported a similar homing tendency by wild cutthroat trout *Salmo clarki* removed from their home sites and liberated elsewhere in the same stream, even after several weeks of enforced retention in a new locality. Allen (1951) reported that the majority of wild brown trout captured, tagged, and released in the Horokiwi Stream, New Zealand, were recaptured either at the point where they were initially captured or within a hundred or so meters of it. He noticed that brown trout in different parts of the stream grew at different rates and concluded that the stream population consisted of a linear series of discrete, nonmixing populations. Miller (1957) recorded 67% of recaptures of cutthroat trout in the same pool or within 200 meters of it and concluded that "... each cutthroat trout of Gorge Creek has a home territory not over twenty yards long ... and that the whole life is spent in it." A general lack of movement by yearling and older brown trout also was reported by Solomon and Templeton (1976).

Although the term "home range" is used by many ecologists and behaviorists, there is disagreement over its meaning and how to measure it (Anderson 1982). Burt (1943) defined home range as "that area traversed by the individual in its normal activities of food gathering, mating and caring for young." Wilson (1975) defined it as the area that an animal learns thoroughly and patrols regularly. The home range reported in this study is an estimate of the area an individual wild brown trout used during the time of principal growth, April through November.

There is little doubt that wild brown trout learn the home range thoroughly, and know the location of hiding places or refuge sites. They

proceed directly and with little lost time or energy to such places in deep water, under rocks, or overhanging brush and banks when disturbed from their foraging sites. Similarly they proceed quickly and directly from one discrete foraging site to another. But why do home ranges get smaller as fish get older?

If home-range size were related to food availability, one would expect home ranges to get larger as fish get older. The behavior of the wild brown trout in Spruce Creek suggests that the home ranges of younger fish are larger because older, larger fish are dominant over smaller fish and force them to move about more. Such movement is energetically costly. As a fish grows, its dominance ranking rises, and it is less likely to be displaced from a particular foraging site. One benefit of dominance may be a smaller, less energy-consuming home range.

If one part of the pool yielded a significantly greater amount of food than another, one would expect that the location of the home ranges of the fish would change as they became older and more dominant. But the home ranges of wild brown trout ranging in age from young of the year through 7+ remained substantially the same for as long as three successive summers, even though their rank in the dominance hierarchy rose. When some older fish disappeared (I suspect fish 51 was caught by poachers early in 1979), such "vacancies" were filled by young of the year or yearling fish. Either different parts of the pool do not differ significantly in food availability, as Jenkins (1969) suggested, or the temporal and spatial variability of food supply is so great that the fish cannot detect the difference.

#### *Foraging Sites and Drift-Feeding*

That trout keep to very precise locations has been known for some time (Hoar 1951; Fabricius and Gustafson 1955; Keenleyside 1962; McCormack 1962; Hartman 1963; Elliott 1965; Baily 1966; Frost and Brown 1967; Chaston 1968; Jenkins 1969; Bohlin 1977; Bassett 1978). Indeed, the persistence with which a trout rises time after time in the same spot is at once both the appeal and at times exasperation of the fly fisherman (personal experience). Kalleberg (1958) refers to a Swedish author (Norbäck 1884) as writing "No fish remains for such a long time on its station without moving from there as the river trout ..."



TABLE 7.—Outcome of agonistic encounters between brown trout (identified by number), 1979.

Winning fish	Losing fish																			
	Wild																			
	3	5	7	8	10	11	14	15	23	24	31	32	34	44	51	52	53	54	57	62
Wild																				
3	-					2			1											
5	2	-	2	3								2	2							
7	1	6	-	2					3			11	1	1	1	1				
8				-						1			9			5	4		3	
10				5	-					1	7					4				
11						-			1							3	14			
14	3	1	1	1	1		-		1		1	1	6			2	1			
15		1						-					3		2					
23				1		4			-		2					2	4			1
24				1						-	1								1	
31				4					1		-	3	1			2	12	2	1	
32				39		2				1	1	-		1					2	
34				9		1	1					8	-			6				
44			1										1	-						
51		2	2				1					2	7		-	1	1			
52																-	1			
53				2													-	3		
54																		-		
57																			-	
62																	1			-
Hatchery																				
81				8														7		
84																				
88													2							
95*		5		17					3		3	4	2		4	2	2	1		
Total losses	6	13	6	92	1	9	2	0	10	3	15	31	34	2	7	28	47	6	7	1

\* Number 95 was assigned to unidentified hatchery brown trout.

In describing the behavior of juvenile Atlantic salmon *Salmo salar* and brown trout in a stream aquarium, Kalleberg (1958) reported "The territorial conditions of the juvenile salmon and brown trout are characterized in a high degree by the fact that each individual possesses within its territory one strongly dominating, strictly localized station. There the fish spends the greater part of its time, from there it defends its territory, and this is the starting point for its feeding excursions."

There is considerable variance and uncertainty in the literature about the meaning of such terms as "station" (Kalleberg 1958; Keenleyside and Yamamoto 1962; McCormack 1962; Bassett 1978; McNicol and Noakes 1981), "home station" (Slaney and Northcote 1974), "position" (Keenleyside 1962; Jenkins 1969), "holding position" (Feldmeth and Jenkins 1973), "microhabitat" (Baltes and Vincent 1969), "lie"

(Frost and Brown 1967), "focal point" (Griffith 1972, 1974; Fausch 1981; Fausch and White 1981), and "territorial focal point" (Everest and Chapman 1972).

Explanations for why salmonids in streams exhibit such localized behavior usually are based on inferences that the locations chosen enable the fish to capture food efficiently and to avoid predation. In this study, I distinguished between those locations the wild brown trout used when drift-feeding (foraging sites), and those sites used when not feeding (refuge sites). The energy-saving utility of foraging sites is evident from the comparative tail-beat frequencies when the fish are waiting in the site, and from the time and effort required to return to the site after each feeding excursion. While the gross location of foraging sites may be influenced by drift patterns (Jenkins 1969), the lack of correlation between site utilization and feeding



TABLE 7.—Extended.

Winning fish	Losing fish				Total wins
	Hatchery				
	81	84	88	95*	
Wild					
3					3
5				6	17
7					27
8				2	24
10					17
11					18
14					19
15				3	9
23					14
24					3
31				9	35
32				1	47
34					25
44					2
51					16
52					1
53					5
54					0
57					0
62					1
Hatchery					
81	-			2	10
84		-			7
88			-	2	4
95*		6		58	105
Total losses	0	6	0	83	409

rates, dominance ranking, and distance to cover suggests that drift patterns, if present, have little effect on site selection.

Another benefit associated with foraging sites may be that the brown trout use the energy in the current to intercept food in the drift. By a relatively small movement of pectoral fins and a flick of the caudal fin, the fish's head is raised into the overhead slipstream. The movement, as revealed in slow-motion videotapes and cinematography suggests that the differential flow over the head and anterior part of the body produces a Bernoulli effect, aiding the fish to capture food with less energy. Energy maximization should be a powerful selection pressure (Fausch and White 1981; Bachman 1982). I suggest that foraging sites are chosen primarily for their energy-saving utility and that at high population densities, foraging sites are a limiting factor. Agonistic encounters associated with foraging sites but not with refuge sites in Spruce Creek support this hypothesis.

Selectivity and size-dependent feeding in a lotic environment has been demonstrated in the case of brook trout (Allan 1978, 1981), juvenile coho salmon *Oncorhynchus kisutch* (Dunbrack and Dill 1983), rainbow trout (Metz 1974; Bisson 1978), and brown trout (Nilsson 1957; Elliott 1967a; Ringler 1979) from stomach-sample analyses. Butler and Hawthorne (1968) reported that large brown trout frequently tolerate smaller trout downstream of them, but never upstream. McNicol and Noakes (1981) showed that the area in which agonistic behavior of juvenile brook trout took place was chordate in shape with the resident stationed at the downstream end facing into the current. A possible explanation for size-dependent food selectivity and the age-dependent decline in feeding rate of the wild brown trout in Spruce Creek is that older, larger fish may pass up smaller items in the drift that would not compensate for the energy expended in capturing them.

#### Dominance Hierarchies

In studies in which the relationships of neighboring brown trout have been directly observed (Jenkins 1969; Bassett 1978; McLaren 1979; present study), dominance was correlated with the age (size) of the fish, but little or no prior residence effect was evident. Neither was there a clear correlation between dominance and position choice, feeding rate, agonistic encounter rate, or distance to cover. In short, the dominant individual appears to have no preferential access to any "best area." So what purpose does the linear hierarchy serve?

The establishment of hierarchies should minimize energy expenditure in the long run. Brown trout normally feed on drift items one by one. If two or more fish were to pursue the same item, at most only one would obtain a benefit to offset its cost. In a lotic environment, the energetic cost associated with drift-feeding is considerable. It is apparently less costly to periodically engage in dominance contests than to scramble for food as each item drifts into view. This is, of course, similar to the arguments used by MacArthur (1972) and Wilson (1975) in showing that territoriality is less costly than pure scramble in defense of food resources.

Li and Brocksen (1977) found that certain subdominant rainbow trout grew faster than the alpha (dominant) individual. A possible ex-



TABLE 8.—Outcome of agonistic encounters between brown trout (identified by number), 1980.

Winning fish	Losing fish																	Total wins				
	Wild										Hatchery											
	3	8	10	11	14	15	30	31	32	36	37	53	54	57	91	92	93		94	95 <sup>a</sup>	96	97
Wild																						
3	-											1							1			2
8		-		2			3		8			8		2	3	1			4			31
10			5	-					2													7
11	1				-					3		1		1	1			1	3	1		12
14	1				3	-													1			5
15	1	1				-						3			5	1		1	12			24
30			1				-				1											2
31		8					9	-	18	20	1		4	7	3			1	4			75
32								1	-	1		3	1	4	1				1			12
36							4			-			1									5
37							1				-											1
53							3				1	-							5			9
54										2		1	-						1			4
57		1					3		1	8	1	3	5	-	4		3		1	2	1	33
Hatchery																						
91							2		2	9	8	1		9	-							31
92				2			1			1	4	1			1	-			1			11
93										2							-		1			3
94						1												-				1
95 <sup>a</sup>	1	3		1			1			1			1						21			29
96												4								-		4
97																		1	1	1		3
Total losses	4	19	0	8	1	0	27	1	31	47	16	26	12	23	18	2	3	4	57	4	1	304

\* Number 95 was assigned to unidentified hatchery brown trout.

planation, but by no means the only one, is that in the confined space of an aquarium a dominant (largest) fish expends too much energy when repeatedly confronted by roving subdominants. At Spruce Creek, higher-ranking wild brown trout, after having repeatedly run off, or defeated, lower-ranking individuals, occasionally did not return immediately to the site at which the agon was initiated, but rather moved to another foraging site. Although anecdotal, such observations suggest that the dominant fish may have moved to another site simply because it was too costly to continue to use the former site.

I believe that agonistic behavior at foraging sites results in the establishment of dominance hierarchies, and that the behavior, when observed over a relatively short period of time gives the impression of territoriality.

#### Territoriality

Noble's (1939) definition of a territory, "any defended area," is in common use today (Ito 1978), although Wilson (1975) defines it some-

what differently by emphasizing exclusivity—"An area occupied more or less exclusively by an animal or group of animals by means of repulsion through overt defense or advertisement." Davies (1978) gives a much broader definition, and recognizes a territory whenever individual animals or groups are spread out more than would be expected from a random occupation of suitable habitats.

Hixon (1980), on the other hand, takes a much narrower view in the definition of territory as "the nearly exclusive access to and utilization of food resources within a mobile animal's home range as a direct result of that animal's aggressive and/or ritualized expulsion of individual food competitors."

Because salmonids are at times difficult to observe directly and identify individually, indirect methods usually have been used to document territoriality. Many authors simply infer territoriality from the observations of stationariness or limited home range (Allen 1951; Fabricius and Gustafson 1955; Newman 1956; Latta 1965; Burnet 1969; Le Cren 1973; Bohlin 1977, 1978).



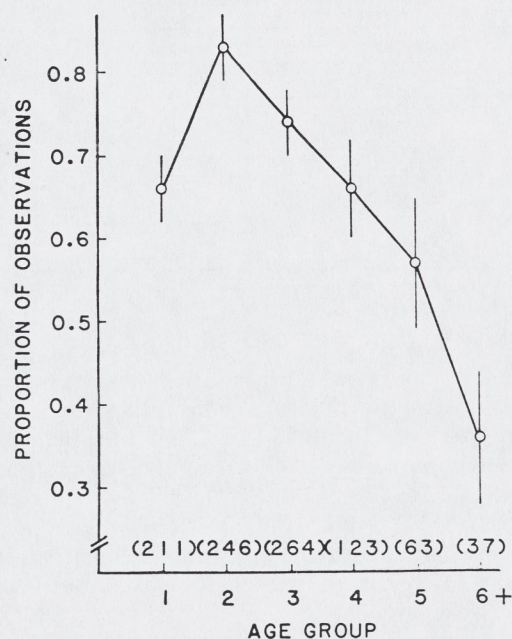


FIGURE 16.—Mean proportion of daily scan observations in which individuals of different age groups were sighted, given that the individual was observed at least once during an observation day; 95% confidence interval is shown by vertical bars. Number of observations for each age group is in parentheses.

Others would maintain that aggressive behavior coupled with stationariness implies territoriality (Stringer and Hoar 1955; Lindroth 1956; Moyle 1969; Slaney and Northcote 1974; Dill 1978). Some make little distinction between territoriality and dominance (Chapman 1962; Keenleyside and Yamamoto 1962; Symons 1971; Li and Brocksen 1977), and Chapman (1966) implied that territories develop in riffles but hierarchies in pools. Noakes (1978), in a general review,

TABLE 10.—Tail-beat frequencies of wild brown trout during various activities in Spruce Creek.

Activity	Mean tail beats per second $\pm$ SE	Number of observations
Sit and wait	0.4 $\pm$ 0.0	45
Return from midwater feed	1.8 $\pm$ 0.7	11
Return from surface feed	2.3 $\pm$ 0.7	43
Stationary swimming near surface	3.0 $\pm$ 0.6	5

suggested that dominance may grade into site-dependent dominance, territoriality, or both, a concept described as scaling in aggressive behavior by Wilson (1975).

Perhaps no other paper is more frequently cited in regard to territoriality of salmonids than Kalleberg's of 1958. It was the first study in which an attempt was made to directly observe and measure the size of individual territories. Kalleberg estimated the size of territories of juvenile Atlantic salmon in a stream aquarium by the distance at which individuals responded aggressively to neighbors and dummies and by "dividing a representative part of the bottom surface by the number of fishes which there defend territories." He implied that each individual had only one station but allowed the possibility of "secondary centres." Not all Atlantic salmon occupied fixed stations. More of them "defended" territories when the water velocity in the tank was increased, and the addition of large rocks produced a similar increase in the number of "territorial" fish. He attributed this change to "visual isolation," although figures accompanying his article show that many of the juvenile salmon had stations on top of the large rocks.

TABLE 9.—Activity durations for wild brown trout in Spruce Creek. Data are mean seconds  $\pm$  SE, derived from analysis of video tapes.

Activity	Number of observations	Pursuit time	Time to return	Total
Feeding				
Surface	39	1.0 $\pm$ 0.1	6.0 $\pm$ 0.3	7.0 $\pm$ 0.4
Midwater	33	1.0 $\pm$ 0.1	3.8 $\pm$ 0.4	4.9 $\pm$ 0.5
Bottom	13	1.0 $\pm$ 0.1	2.7 $\pm$ 0.5	3.8 $\pm$ 0.5
False feed	24			2.5 $\pm$ 0.3
Agonistic encounters	21			13.7 $\pm$ 1.1



TABLE 11.—Age-related distribution of activity times (%) for wild brown trout in Spruce Creek, 0900–1900 hours.

Activity	Age group						Weighted mean <sup>a</sup>
	1	2	3	4	5	6+	
Pursuit	3.9	3.4	2.9	2.8	1.8	1.0	3.1
Return to site	10.1	9.5	7.8	7.7	4.9	2.6	8.4
Position change	1.3	1.7	1.7	0.7	1.1	1.0	1.4
Agonistic encounters	0.6	0.8	0.8	0.9	1.4	1.2	0.9
Gape	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Sit and wait	84.0	84.5	86.8	87.8	90.8	91.1	86.2

<sup>a</sup> Weighted for age group.

I believe that the behavior described by Kalleberg (1958) can be more easily and parsimoniously explained as an energy-minimizing response. When water velocities are high, fish cannot afford to pursue food or attack intruders at as great a distance as when velocities are low. The addition of large rocks may well have simply added more energy-saving sites. Stationariness accompanied by aggressive behavior, I believe, is not sufficient to define territoriality.

Ito (1978) and Noakes (1978) distinguished between territoriality and hierarchies on the basis of prior residence. Noakes (1978) stated, "We must have individual identification of the fish within a group, and evidence that dominance is independent of location within the study area, before reasonably concluding that a dominance hierarchy is present." and Ito (1978) stated, "... in a conflict over a territory the characteristic of territoriality is, that, unlike social hierarchies seen within groups of non-territorial species, the territory holder wins the fight as a rule even if he is smaller than the intruder. This is called the effect of prior residence." If prior residence can be considered to be a formal test of territoriality, then the wild brown trout at Spruce Creek were not territorial. That the outcome of agonistic encounters among wild trout was not site-dependent is attested to by the remarkably linear social structure observed, with few reversals or ambiguities, and the stability of the structure from year to year. The introduction of hatchery brown trout further demonstrated that no prior resident effect was evident and that the outcome of agonistic encounters was primarily a function of size.

Bohlin (1977) claimed that resident age-1+ wild brown trout had an owner's advantage over

wild age-1+ brown trout introduced into an experimental area from downstream, but the results might just as easily be explained by a homing tendency of the introduced fish (Schuck 1945).

Nice (1941) defined six major types of territory according to the function involved. Wilson (1975) modified these slightly and described five types labeled, A through E, that depended on various mixes of mating, nesting, resting, and foraging activities. Ito (1978) introduced a new Type F territory, a defended area in which the food supply is guaranteed, whether for reproduction or not. Wilson (1975) disagreed with those who would define territory in terms of economic function (Pitelka 1959), and sided with those who define territory by the mechanism through which exclusiveness is maintained.

All of the brown trout in Spruce Creek used more than one foraging site in a day and none of the sites was used exclusively by only one fish. No fish had an exclusive home range or foraging site, so neither the home range nor the area surrounding the foraging sites would pass the exclusivity test for territoriality.

One could argue, of course, that each foraging site held by the fish is a "partial" (Greenberg 1947), "floating" or "spatio-temporal" territory (Wilson 1975). One could add to the confusion by coining yet another term "pseudo-territory." I suggest instead that none of these terms confers any more information than merely stating that foraging sites are energetically efficient and that the agonistic behavior associated with foraging sites is a cost-minimizing phenomenon. I suggest that the term territoriality may be meaningless as generally applied to stream-living salmonids (with the possible exception of the ayu *Plecoglossus altivelis*; Kawa-



TABLE 12.—Comparative activity of wild and hatchery brown trout in Spruce Creek, 1979 and 1980.

Activity	Type of fish	Mean number per 15 minutes $\pm$ SE	Data transformation	Number of 15-minute observation periods	P (t-test)	Proportion of non-zero observations	P (binomial)
<i>Late summer 1979</i>							
Feeding Surface	Wild	4.7 $\pm$ 1.0		63		0.70	
	Hatchery	0.3 $\pm$ 0.1	Log <sub>e</sub>	62	<0.01	0.16	0.01
Midwater	Wild	3.4 $\pm$ 0.5		63		0.70	
	Hatchery	1.8 $\pm$ 0.4	Log <sub>e</sub>	62	>0.20	0.46	0.01
Bottom	Wild	1.0 $\pm$ 0.2		63		0.41	
	Hatchery	0.3 $\pm$ 0.1	Log <sub>e</sub>	62	0.06	0.16	0.01
Total	Wild	9.2 $\pm$ 1.2		63		0.89	
	Hatchery	2.4 $\pm$ 3.5	Log <sub>e</sub>	62	<0.01	0.60	0.01
Agonistic encounters	Wild	1.7 $\pm$ 0.4		63		0.43	
	Hatchery	3.4 $\pm$ 0.7	Log <sub>e</sub>	62	0.06	0.57	0.10
Gape	Wild	0.4 $\pm$ 0.1		63		0.81	
	Hatchery	0.3 $\pm$ 0.1	Square root	62	>0.20	0.84	>0.20
Moves	Wild	3.1 $\pm$ 0.6		63		0.62	
	Hatchery	10.4 $\pm$ 2.1	Log <sub>e</sub>	62	<0.01	0.77	0.06
<i>Spring 1980</i>							
Feeding Surface	Wild	9.4 $\pm$ 0.8		152		0.86	
	Hatchery	4.8 $\pm$ 0.6	Square root	98	0.03	0.61	0.01
Midwater	Wild	8.2 $\pm$ 0.8		152		0.89	
	Hatchery	4.2 $\pm$ 0.4	Log <sub>e</sub>	98	<0.01	0.79	0.04
Bottom	Wild	1.8 $\pm$ 0.2		152		0.62	
	Hatchery	1.6 $\pm$ 0.3	None	98	>0.20	0.49	0.04
Total	Wild	19.4 $\pm$ 1.3		152		0.98	
	Hatchery	10.6 $\pm$ 0.9	Square root	98	<0.01	0.87	0.02
Agonistic encounters	Wild	1.7 $\pm$ 0.2		152		0.53	
	Hatchery	2.2 $\pm$ 0.6	None	98	>0.20	0.46	>0.20
Gape	Wild	0.8 $\pm$ 0.1		152		0.55	
	Hatchery	0.6 $\pm$ 0.1	None	98	0.11	0.36	0.01
Moves	Wild	3.2 $\pm$ 0.4		152		0.60	
	Hatchery	4.4 $\pm$ 0.7	Log <sub>e</sub>	98	0.01	0.53	>0.20

nabe 1969) and that it carries with it certain connotations that so far have not been supported by field observations.

#### *Growth*

We would expect to find the reproductive success of salmonids to be highly correlated with size. Larger fish have more and larger eggs (Frost and Brown 1967; Weatherly and Rogers 1978), and larger eggs produce larger young that, in turn, have better growth and survival (Lagler et al. 1962; Frost and Brown 1967; Bagenal 1969). Size is also an important factor in competition among males during the spawning

season (Frost and Brown 1967; Butler and Hawthorne 1975; personal observation). Consequently, there should be a strong selective pressure for rapid and sustained growth among salmonids.

But growth typically is found to be asymptotic, the upper limit of growth differing from one stream to another. This leads us to search for physiological and environmental factors that determine growth rates and upper limits to growth.

In streams such as Spruce Creek, certain species of salmonids may derive the majority of their food from drift (Müller 1954; Nilsson 1957;



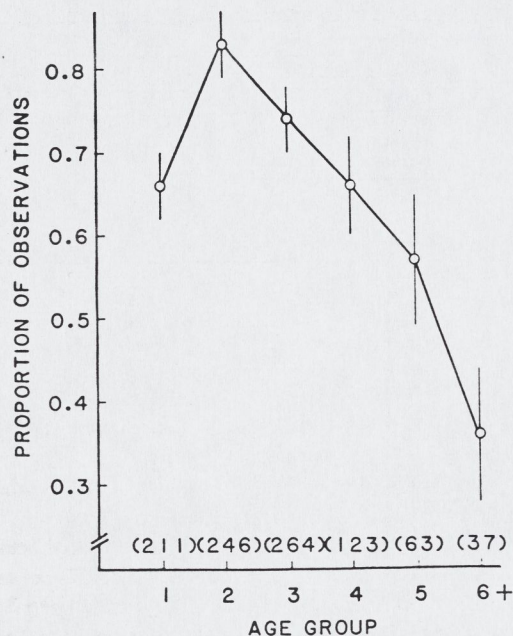


FIGURE 16.—Mean proportion of daily scan observations in which individuals of different age groups were sighted, given that the individual was observed at least once during an observation day; 95% confidence interval is shown by vertical bars. Number of observations for each age group is in parentheses.

Others would maintain that aggressive behavior coupled with stationariness implies territoriality (Stringer and Hoar 1955; Lindroth 1956; Moyle 1969; Slaney and Northcote 1974; Dill 1978). Some make little distinction between territoriality and dominance (Chapman 1962; Keenleyside and Yamamoto 1962; Symons 1971; Li and Brocksen 1977), and Chapman (1966) implied that territories develop in riffles but hierarchies in pools. Noakes (1978), in a general review,

TABLE 10.—Tail-beat frequencies of wild brown trout during various activities in Spruce Creek.

Activity	Mean tail beats per second $\pm$ SE	Number of observations
Sit and wait	$0.4 \pm 0.0$	45
Return from midwater feed	$1.8 \pm 0.7$	11
Return from surface feed	$2.3 \pm 0.7$	43
Stationary swimming near surface	$3.0 \pm 0.6$	5

suggested that dominance may grade into site-dependent dominance, territoriality, or both, a concept described as scaling in aggressive behavior by Wilson (1975).

Perhaps no other paper is more frequently cited in regard to territoriality of salmonids than Kalleberg's of 1958. It was the first study in which an attempt was made to directly observe and measure the size of individual territories. Kalleberg estimated the size of territories of juvenile Atlantic salmon in a stream aquarium by the distance at which individuals responded aggressively to neighbors and dummies and by "dividing a representative part of the bottom surface by the number of fishes which there defend territories." He implied that each individual had only one station but allowed the possibility of "secondary centres." Not all Atlantic salmon occupied fixed stations. More of them "defended" territories when the water velocity in the tank was increased, and the addition of large rocks produced a similar increase in the number of "territorial" fish. He attributed this change to "visual isolation," although figures accompanying his article show that many of the juvenile salmon had stations on top of the large rocks.

TABLE 9.—Activity durations for wild brown trout in Spruce Creek. Data are mean seconds  $\pm$  SE, derived from analysis of video tapes.

Activity	Number of observations	Pursuit time	Time to return	Total
Feeding				
Surface	39	$1.0 \pm 0.1$	$6.0 \pm 0.3$	$7.0 \pm 0.4$
Midwater	33	$1.0 \pm 0.1$	$3.8 \pm 0.4$	$4.9 \pm 0.5$
Bottom	13	$1.0 \pm 0.1$	$2.7 \pm 0.5$	$3.8 \pm 0.5$
False feed	24			$2.5 \pm 0.3$
Agonistic encounters	21			$13.7 \pm 1.1$



TABLE 11.—Age-related distribution of activity times (%) for wild brown trout in Spruce Creek, 0900–1900 hours.

Activity	Age group						Weighted mean <sup>a</sup>
	1	2	3	4	5	6+	
Pursuit	3.9	3.4	2.9	2.8	1.8	1.0	3.1
Return to site	10.1	9.5	7.8	7.7	4.9	2.6	8.4
Position change	1.3	1.7	1.7	0.7	1.1	1.0	1.4
Agonistic encounters	0.6	0.8	0.8	0.9	1.4	1.2	0.9
Gape	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Sit and wait	84.0	84.5	86.8	87.8	90.8	91.1	86.2

<sup>a</sup> Weighted for age group.

I believe that the behavior described by Kal-leberg (1958) can be more easily and parsimoniously explained as an energy-minimizing response. When water velocities are high, fish cannot afford to pursue food or attack intruders at as great a distance as when velocities are low. The addition of large rocks may well have simply added more energy-saving sites. Stationariness accompanied by aggressive behavior, I believe, is not sufficient to define territoriality.

Ito (1978) and Noakes (1978) distinguished between territoriality and hierarchies on the basis of prior residence. Noakes (1978) stated, "We must have individual identification of the fish within a group, and evidence that dominance is independent of location within the study area, before reasonably concluding that a dominance hierarchy is present." and Ito (1978) stated, "... in a conflict over a territory the characteristic of territoriality is, that, unlike social hierarchies seen within groups of non-territorial species, the territory holder wins the fight as a rule even if he is smaller than the intruder. This is called the effect of prior residence." If prior residence can be considered to be a formal test of territoriality, then the wild brown trout at Spruce Creek were not territorial. That the outcome of agonistic encounters among wild trout was not site-dependent is attested to by the remarkably linear social structure observed, with few reversals or ambiguities, and the stability of the structure from year to year. The introduction of hatchery brown trout further demonstrated that no prior resident effect was evident and that the outcome of agonistic encounters was primarily a function of size.

Bohlin (1977) claimed that resident age-1+ wild brown trout had an owner's advantage over

wild age-1+ brown trout introduced into an experimental area from downstream, but the results might just as easily be explained by a homing tendency of the introduced fish (Schuck 1945).

Nice (1941) defined six major types of territory according to the function involved. Wilson (1975) modified these slightly and described five types labeled, A through E, that depended on various mixes of mating, nesting, resting, and foraging activities. Ito (1978) introduced a new Type F territory, a defended area in which the food supply is guaranteed, whether for reproduction or not. Wilson (1975) disagreed with those who would define territory in terms of economic function (Pitelka 1959), and sided with those who define territory by the mechanism through which exclusiveness is maintained.

All of the brown trout in Spruce Creek used more than one foraging site in a day and none of the sites was used exclusively by only one fish. No fish had an exclusive home range or foraging site, so neither the home range nor the area surrounding the foraging sites would pass the exclusivity test for territoriality.

One could argue, of course, that each foraging site held by the fish is a "partial" (Greenberg 1947), "floating" or "spatio-temporal" territory (Wilson 1975). One could add to the confusion by coining yet another term "pseudo-territory." I suggest instead that none of these terms confers any more information than merely stating that foraging sites are energetically efficient and that the agonistic behavior associated with foraging sites is a cost-minimizing phenomenon. I suggest that the term territoriality may be meaningless as generally applied to stream-living salmonids (with the possible exception of the ayu *Plecoglossus altivelis*: Kawa-



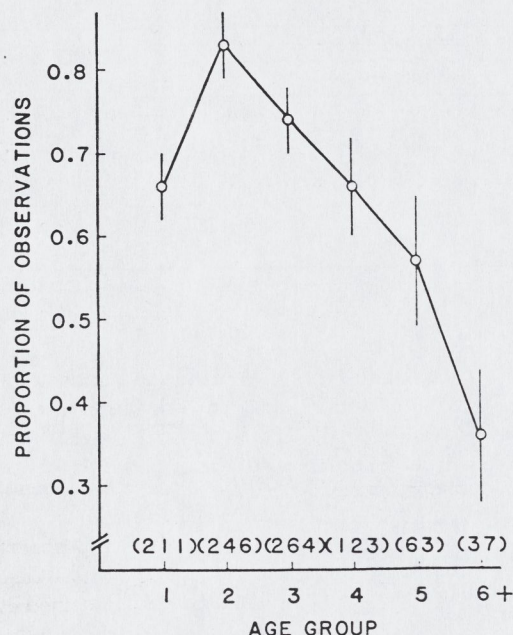


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False feed	24			$2.5 \pm 0.3$
Agonistic encounters	21			$13.7 \pm 1.1$



TABLE 12.—Comparative activity of wild and hatchery brown trout in Spruce Creek, 1979 and 1980.

Activity	Type of fish	Mean number per 15 minutes $\pm$ SE	Data transformation	Number of 15-minute observation periods	P (t-test)	Proportion of non-zero observations	P (binomial)
Late summer 1979							
Feeding Surface	Wild	4.7 $\pm$ 1.0	Log <sub>e</sub>	63	<0.01	0.70	0.01
	Hatchery	0.3 $\pm$ 0.1		62		0.16	
Midwater	Wild	3.4 $\pm$ 0.5	Log <sub>e</sub>	63	>0.20	0.70	0.01
	Hatchery	1.8 $\pm$ 0.4		62		0.46	
Bottom	Wild	1.0 $\pm$ 0.2	Log <sub>e</sub>	63	0.06	0.41	0.01
	Hatchery	0.3 $\pm$ 0.1		62		0.16	
Total	Wild	9.2 $\pm$ 1.2	Log <sub>e</sub>	63	<0.01	0.89	0.01
	Hatchery	2.4 $\pm$ 3.5		62		0.60	
Agonistic encounters	Wild	1.7 $\pm$ 0.4	Log <sub>e</sub>	63	0.06	0.43	0.10
	Hatchery	3.4 $\pm$ 0.7		62		0.57	
Gape	Wild	0.4 $\pm$ 0.1	Square root	63	>0.20	0.81	>0.20
	Hatchery	0.3 $\pm$ 0.1		62		0.84	
Moves	Wild	3.1 $\pm$ 0.6	Log <sub>e</sub>	63	<0.01	0.62	0.06
	Hatchery	10.4 $\pm$ 2.1		62		0.77	
Spring 1980							
Feeding Surface	Wild	9.4 $\pm$ 0.8	Square root	152	0.03	0.86	0.01
	Hatchery	4.8 $\pm$ 0.6		98		0.61	
Midwater	Wild	8.2 $\pm$ 0.8	Log <sub>e</sub>	152	<0.01	0.89	0.04
	Hatchery	4.2 $\pm$ 0.4		98		0.79	
Bottom	Wild	1.8 $\pm$ 0.2	None	152	>0.20	0.62	0.04
	Hatchery	1.6 $\pm$ 0.3		98		0.49	
Total	Wild	19.4 $\pm$ 1.3	Square root	152	<0.01	0.98	0.02
	Hatchery	10.6 $\pm$ 0.9		98		0.87	
Agonistic encounters	Wild	1.7 $\pm$ 0.2	None	152	>0.20	0.53	>0.20
	Hatchery	2.2 $\pm$ 0.6		98		0.46	
Gape	Wild	0.8 $\pm$ 0.1	None	152	0.11	0.55	0.01
	Hatchery	0.6 $\pm$ 0.1		98		0.36	
Moves	Wild	3.2 $\pm$ 0.4	Log <sub>e</sub>	152	0.01	0.60	>0.20
	Hatchery	4.4 $\pm$ 0.7		98		0.53	

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#### Growth

We would expect to find the reproductive success of salmonids to be highly correlated with size. Larger fish have more and larger eggs (Frost and Brown 1967; Weatherly and Rogers 1978), and larger eggs produce larger young that, in turn, have better growth and survival (Lagler et al. 1962; Frost and Brown 1967; Bagenal 1969). Size is also an important factor in competition among males during the spawning

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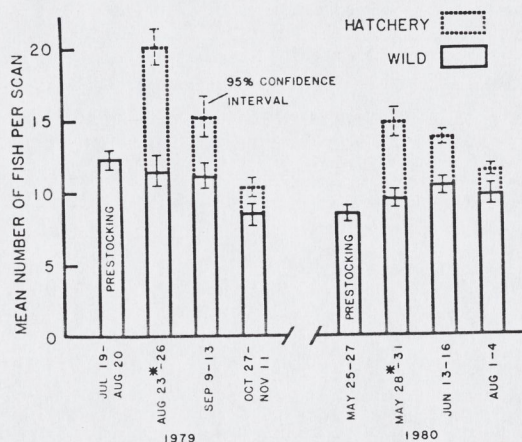


FIGURE 17.—Mean number of wild and hatchery brown trout seen during hourly scan observations in 1979 and 1980. Stocking dates (\*) were August 23, 1979, and May 28, 1980.

Elliott 1967b; Waters 1969; Griffith 1974). Although the numbers and biomass of drift organisms in streams are spatially and temporally quite variable (Elliott 1967b; Lehmkuhl and Anderson 1972; Reisen and Prins 1972; Waters 1972; Bisson 1978) it appears that the mean amount of drift that passes a particular point in a stream is, over the long run, a linear function of the velocity at that point (Elliott 1967b; Chapman and Bjornn 1969). The metabolic rate, or amount of energy expended per unit time by salmonids, on the other hand, is an exponential function of swimming speed (Brett 1964; Rao 1968).

I previously showed (Bachman 1982) that these environmental and physiological constraints set a size-dependent optimum velocity for drift-feeding fish. At the optimum velocity, growth rate should be maximal. According to this model, larger drift-feeding fish should grow faster in slower water, and a fish that remains a drift feeder should ultimately grow to a size at which the energy in the drift just equals the energy expended in capturing food, producing gametes, and reproductive behavior.

As a first approximation, then, the growth rate of individual fish should be determined by the differential energy between that obtained from the drift in a fish's home range and the energy it expends to obtain it. Because drift densities vary from stream to stream and from place to place within a stream, and because many

salmonids spend most of their lives in one small section of a stream (Schuck 1945; Allen 1951; Miller 1954a, 1957; present study), different places should grow different size fish and at different rates. Brown trout (Allen 1951), brook trout (Cooper et al. 1962), and cutthroat trout (Cooper 1970) have all been reported growing faster in the lower parts of a stream than in the upper parts.

It may be that large trout are repeatedly captured at the same places in a stream because those places grow larger fish rather than attract larger fish. This idea is supported by the observation that when a few large brown trout disappeared from the observation area in the spring of 1980 (there was some evidence of poaching at the time) the feeding sites formerly occupied by an age-5 fish (number 51) subsequently were occupied by a yearling.

If population densities, as I have suggested, are determined primarily by the number of suitable foraging sites, and the growth rates are determined by the energy differential at those foraging sites, what might be the density effect on growth?

If the rate at which drift-feeding fish take food from the current is very much smaller than the rate the food enters and leaves the water from the surface and the bottom, growth rates should be independent of population density. Although few data exist on the rates food enters and leaves the drift, because such rates are so hard to measure, there is evidence of density-independent growth by coho salmon (Chapman 1965), brook trout (Cooper et al. 1962), and brown trout (Mortensen 1982).

#### Gaping

The gape reflex of wild and hatchery brown trout appears to be a comfort movement induced by the buildup of  $\text{CO}_2$  in the bloodstream. Two factors theoretically would affect blood  $\text{CO}_2$  concentrations, metabolic rate and  $\text{CO}_2$  concentrations in the water. The positive correlation of gape rate with temperature, the high gape rates in summer, and the sharp rise in gape rate in mid-afternoon appear to reflect the temperature effect on metabolic rate. The morning decrease in gape rate probably reflects a drop in dissolved  $\text{CO}_2$  in the water associated with photosynthetic activity of macrophytes and algae in the stream. The temporal gaping pattern evident by both wild and hatchery brown



trout suggests that this may be a fruitful area for further research.

#### *Hatchery and Wild Trout Compared*

The poor survival of hatchery trout in streams is well documented (Hoover and Johnson 1938; Hazzard and Shetter 1939; Shetter and Hazzard 1941; Needham and Slater 1944, 1945; Schuck 1945, 1948; Smith and Smith 1945; Shetter 1947; Cooper 1953, 1959; Miller 1958; Mason et al. 1967; Millard and MacCrimmon 1972), but there is no consensus as to the cause. Schuck (1948) listed ten possible causes, ranging from environmental factors such as insufficient food, high water temperature, and predation to management practices including planting methods, hatchery diets, lack of exercise in the hatchery, and domestication. Miller (1952, 1958) attributed weight loss and mortality of hatchery-reared cutthroat trout stocked in Alberta streams to competition with wild trout and showed that hatchery fish stocked in a stream that contained wild fish had higher lactic-acid concentrations in the blood than did hatchery cutthroat trout not in "competition" with wild fish. Nielsen et al. (1957), on the other hand, reported that differences in stocking densities of hatchery rainbow trout had no effect on the survival of the stocked fish and concluded that competition with wild brown trout was *not* a cause of mortality among hatchery-reared trout. Miller (1954b) and Vincent (1960) suggested that selection in the hatchery produces domesticated fish that cannot survive well in streams.

In work with juvenile Atlantic salmon, Fenderson et al. (1968) proposed that unnaturally high aggressiveness in hatchery stocks may contribute to mortality through loss of feeding time, excessive expenditure of energy, and increased exposure to predators. Jenkins (1971) came to much the same conclusion, suggesting that the behavioral patterns of domesticated trout, successful in a crowded hatchery raceway, are wasteful of energy and ill-adapted to the conditions in a natural environment. Even when the return of stocked trout to anglers is high, and a large fraction are taken within a few weeks of planting, the natural mortality rate (or "unaccounted mortality"), as reflected in the number of trout lost due to causes other than angling, may be very high (Butler and Borgeson 1965).

The results of my study at Spruce Creek support the hypothesis that a contributing cause of mortality among hatchery trout is excessive expenditure of energy. The hatchery brown trout moved more frequently, were less likely to use energy-efficient foraging sites, and engaged in more agonistic encounters than the wild brown trout. Although hatchery brown trout won as many agonies as they lost, they were less likely to return to the location where the agon was initiated than were wild fish. The lack of identification with any particular geographic location and the attendant failure to become integrated into a long-term social structure also must be costly to hatchery fish.

Hatchery brown trout fed much less than did wild brown trout, a factor that would aggravate the already adverse energy balance. In contrast, McLaren (1979) reported that wild brown trout from Spruce Creek, transported, tagged, and stocked in hatchery raceways, fed less frequently than hatchery brown trout subjected to the same treatment. This suggests that wild brown trout may be more stressed by handling and new surroundings than hatchery brown trout.

The reason the hatchery fish in my study fed less than the wild fish may be that it takes a considerable time for hatchery brown trout to learn to feed on natural food and some may never learn. Elliott (1975) showed that some hatchery brown trout refused to eat or took only a small number of natural food items in a feeding experiment. Ersbak and Haase (1983) found that wild brown trout ate nearly twice as much food as hatchery-reared brook trout in McMichael Creek, Pennsylvania, and concluded that the stocked brook trout were unable to obtain sufficient food for survival in the stream they studied.

Other factors that may account for poor survival of hatchery trout in streams are size and condition. Klak (1941), Needham and Slater (1945), Miller (1952, 1954b, 1958), Reimers (1963), Hunt and Jones (1972), and Ersbak and Haase (1983) all reported a decline in condition factor of hatchery trout stocked in streams. Ersbak and Haase (1983) also showed that the higher the coefficient of condition when stocked, the faster it declined. According to the energy-balance model for drift-feeding salmonids that I developed (Bachman 1982), there is an upper size limit that a drift-feeding salmonid can attain in a particular environment and population



density has little or no effect on that limit. The hatchery brown trout in Spruce Creek were, like the wild brown trout, drift feeders. One reason many hatchery trout die may be that they are too big for the stream in which they are stocked. It seems unreasonable to expect a 35-cm hatchery trout to survive in a stream where the average wild trout rarely exceeds 30 cm.

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# World Distribution of Brown Trout, *Salmo trutta*<sup>1</sup>

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## ABSTRACT

During the past century the Eurasian and North African range of the brown trout, *Salmo trutta* L., has been extended to include discontinuous populations on all continents except Antarctica. Primary factors affecting the establishment of naturalized populations are water temperature, precipitation, and suitable spawning grounds. Any future major expansion in the world distribution of the brown trout, with the possible exception of Asia, is unlikely.

## INTRODUCTION

DURING THE PAST CENTURY the pristine range of the brown trout, *Salmo trutta* Linnaeus, in Eurasia and North Africa, has been extended through introduction to include waters on all continents except Antarctica.

Linnaeus, when naming the trout of Sweden *Salmo trutta* in 1758, regarded the sea trout (*S. eriox*) and the brook trout (*S. fario*) as distinct species. The latter species must not be confused with the North American brook trout, *Salvelinus fontinalis* (American Fisheries Society, 1960). After that time various local representatives of the genus were given a variety of common and specific names (Regan, 1911) which included the common trout (*S. fario*, *ausonii*, *gairnardi*, *cornubiensis*), the English salmon trout (*S. trutta*, *eriox*, *cambricus*, *albus*, *phinoc*, *brachypoms*), the golden estuarine trout (*S. estuarius*, *orcadensis*, *gallivensis*), the great black lake trout (*S. ferox*, *nigripinnis*), the gillaroo (*S. stomachicus*), and the silver or Loch Leven trout (*S. caecifer*, *levenensis*). The exchange of brown trout stocks among European countries, such as the transfer of German brown trout to England in 1884 (Smiley, 1884) and to Italy in 1885 (Pavesi, 1887), further complicated the problem of speciation.

Modern ichthyologists, however, generally accept the concept of Günther (1866), Regan (1911), Jordan (1926), and Hubbs (1930) that there is but one species, *Salmo trutta*, and that trout with distinctive features should be recognized at only the subspecific level, if at all.

Most populations of brown trout now resident in hatcheries and natural waters throughout the world stem from the following three sources: sea run specimens of the European trout (*Salmo trutta trutta*), European trout permanently resident in fresh water (*Salmo trutta fario*), and the trout (*Salmo trutta levenensis*) from Loch Leven, and other waters of Scotland and northern

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England. Because of interbreeding in fish culture programmes, and the introduction of hybrids or several stocks to many waters, it would seem imprudent for practical purposes to identify the brown trout beyond the specific level (Wiggins, MS, 1950).

The objectives of this paper are: firstly, to present an account of known attempts to introduce the brown trout (*Salmo trutta* L.) beyond its native range; and secondly, to document the present world distribution of the species which has resulted from these introductions.

#### NATIVE RANGE

The native range of the brown trout (Fig. 1) has been established essentially from published material by Seeley (1886), Bean (1888), Dahl (1918,



FIG. 1. Native distribution of *Salmo trutta*.

1919), Berg (1932), Tchernavin (1939), Wiggins (MS, 1950), Nikolskii (1937, 1961), and Vladykov (1931, 1963).

The early distribution of the species is believed to have extended from Iceland and the northern coasts of Europe southward to the countries fronting on the Mediterranean Sea, the islands of Corsica and Sardinia, and Algeria in northern Africa. The range extended eastward from the Atlantic drainage towards the northern slopes of the Himalayas. Migratory brown trout inhabited the Black, Caspian, and Aral seas and their tributaries.



KNOWN INTRODUCTIONS  
AUSTRALIA AND NEW ZEALAND

## AUSTRALIA

The earliest known introduction of the brown trout beyond its native range was a planting made in Tasmania in 1864 (Lake, personal communication).<sup>2</sup> The ova, obtained from the Wey and River Itchen at High Wycombe, left London, England, on January 21, 1864, and arrived in Tasmania 91 days later. Although only some 300 eggs hatched, a small planting made in the Plenty River would seem to have established a naturalized population there. Of a further experiment of 15,000 trout eggs transported to Tasmania in the following year, about 500 fry were hatched (Frost and Brown, 1967). From the progeny of these stocks came widespread introductions into the rivers of Tasmania, mainland Australia, and New Zealand. At present, naturalized populations of brown trout occur in most waters of Tasmania (Lynch, personal communication).

On mainland Australia, the possibility of a second importation from England to Victoria has been noted by Tonbridge (personal communication). Weatherley and Lake (1967) citing Roughley (1951), also indicate that eggs from Tasmanian stocks were distributed in Victoria. Progeny of the Victorian stocks were then introduced into the waters of New South Wales by 1888.

Presently, brown trout occur in tableland streams of the eastern highlands of New South Wales and Victoria above 600 m elevation (Fig. 2). In the case of steep mountain streams they may be found as low as 300 m (Lake, 1957).



FIG. 2. Naturalized distribution of *Salmo trutta* in Australia and New Zealand.

<sup>2</sup>All personnal communications cited in this paper are listed alphabetically after the References section of this paper.



Weatherley and Lake (1967) further note that in the more northern regions of the Highlands in New South Wales, waters below 1200 m provide only a marginal summer existence.

Attempts to introduce brown trout into Queensland began in 1896, when the Government purchased 32,000 ova from New Zealand. To date, the principal areas of introduction have been the Stanthorpe and Warwick districts in the south and the Atherton Tablelands of the north (Haysom, personal communication). The known extent of naturalized populations is limited to the former Districts.

Although no dates of introduction are given, trout (brown or rainbow) also may be found to a limited extent in the Pemberton region of Western Australia and in some small streams near Adelaide, South Australia (Weatherley and Lake, 1967).

#### NEW ZEALAND

In New Zealand, Hobbs (1948) reported that imports from Tasmania continued from at least 1867 to 1875 at which time populations on the South Island, through the effort of societies in Otago and Canterbury provinces, became self-supporting. By 1885, plantings on the North Island had become equally successful.

Little (personal communication) reports that brown trout have since been stocked in almost every conceivable lake, river, or stream, such that the present naturalized distribution encompasses every suitable ecological niche in the confines of New Zealand (Fig. 2). Little also mentions that supplemental private plantings by acclimatization societies have continued in support of the popular sport fishery.

Three thousand brown trout fry sent to the Chatham Islands (1100 km east of New Zealand) failed to survive a voyage there in 1916 or 1917. Further private introductions between 1934 and 1949 also were unsuccessful (Skrynski, 1967).

#### ASIA

##### INDIA

European brown trout were first transplanted to the District of Nilgiris, State of Madras, in 1863. These, and later plantings of the Loch Leven variety between 1866 and 1873, failed to establish populations (Tripathi, personal communication; Wiggins, MS, 1950).

The most important introduction to India was made in 1889 (Table I) when brown trout ova of European origin were hatched in the more northerly State of Kashmir. Here they became firmly established in a number of streams of the Kashmir Valley (Fig. 3) and some 20 years later progeny of these fish were being distributed in the waters of two adjacent southern states, Himachal and Uttar Pradesh (Tripathi, personal communication). Himachal State met with good success in naturalizing the species although unprecedented floods in 1947 were reported to have destroyed river populations in the Chamba



TABLE I. Introductions of brown trout to India.

State/district	Year of introduction	Source	Present status
Madras			
Nilgiris	1863-73	England	Apparent failure
Jammu & Kashmir			
Kashmir	1889	Europe	Well established
Jammu	1963	Kashmir	Not yet known
Nefa	1966	"	Not yet known
Uttar Pradesh			
Kumaon Hills	1910, 1912	"	Not known
Himachal Pradesh			
Mandi	1909	"	Well established
Kulu	1909	"	Well established
Kangra	1911	Kulu	Perished in 1947
Chamba	1919	Kulu	Perished in 1947
Mahasu	1915	Kashmir	Well established
Kinnaur	1963	Kashmir	Well established

and Kangra valleys. Plantings in the Uttar State appear to have met with failure. The result of introductions to Jammu in 1963, and NEFA in 1966 have not yet been appraised.

#### CEYLON

Although records of the earliest plantings were reported to have been lost, approximately 20 brown trout (*Salmo fario*) were liberated in a small stream crossing the plain of Nuwara Eliya in 1892 (Fowke, 1938). Ova of unrecorded origin were imported each year between 1886 and 1889, their disappearance leading to further importations in 1892 and 1893. Brown trout were known to breed only occasionally during exceptionally cold years and for this reason were always "under control" (Fowke, 1938). Fowke further implies that with the failure of brown trout breeding, the culture and distribution of the naturally reproducing rainbow trout, *Salmo gairdneri* (Richardson), have flourished.

#### WEST PAKISTAN

A report of brown trout within 200 km of the Kashmir border lacks confirmation. However, proximity of the flourishing Kashmir populations would offer substantial evidence in favour of the report.

#### JAPAN

Importation of "trout" from the United States took place prior to 1900 (Jordan and Snyder, 1902). Brown trout are presently reared in two research laboratories and two hatcheries from which limited plantings are made to





FIG. 3. Naturalized distribution of *Salmo trutta* in South Central Asia.

local waters, although the species is not valued by the Japanese (Shiraishi, personal communication). The only known naturalized population of brown trout exists in Chuzenji Lake, Nikko City, Tochigi Pref.

#### NORTH AMERICA

##### UNITED STATES OF AMERICA

The original plantings of brown trout into North America came from eggs sent from Germany to New York by Herr Von Behr during the winter of 1883. These eggs were hatched at the Northville Hatchery, Michigan, and the fry released in early April in the Pere Marquette River of northern Michigan (Mather, 1889; Goode, 1903). Limited success followed a second shipment



of Von Behr trout which were again incubated at the Northville Hatchery, and at the Caledonia Hatchery, New York. Further shipments of eggs from Germany between 1884 and 1887 were reared in hatcheries at Cold Spring Harbour and Caledonia, New York; Northville, Michigan; Central Station, Washington; and Wytherville, Virginia (Smiley, 1884). Shipments of German ova were sent, also, to hatcheries in Pennsylvania and New Hampshire (Smiley, 1889a) and by 1897 eggs had been received by hatcheries in California (Anonymous, 1897).

The Loch Leven variety was first imported to the United States in 1885 (Smiley, 1889b). From this first shipment, ova were immediately transferred to hatcheries in Maine, New Hampshire, Iowa, and Minnesota. By 1887 they were being held in hatcheries extending from the states of Maine, Maryland, and Illinois in the east to Colorado and California in the west (Anonymous, 1897). However, because of numerous hatchery transfers, the identity of the German and Loch Leven varieties was soon lost (Miller and Alcorn, 1945).

Apparently more tolerant of environmental conditions than the native brook trout (*Salvelinus fontinalis* Mitchell), the brown trout was accused of serious competition with the former species and a precedent was set in 1906 when New York State sharply reduced the magnitude of its brown trout propagation (Bean, 1906).

In spite of the action of most government agencies in following the policy established by New York State, a survey of all states agencies in 1967 indicates that brown trout were ultimately introduced into 45 of the 50 American states (Table II). In the 34 states which now have naturalized populations in some waters within their boundaries (Fig. 4) all plantings had been made prior to 1936. Although no known naturalized populations of brown trout exist in Delaware, Indiana, Illinois, Missouri, and North Dakota, stocking programs continue. In Florida, Kansas, Oklahoma, Ohio, Kentucky, and Hawaii, failure in naturalization resulted in discontinuation of plantings. Texas, Louisiana, Mississippi, Alabama, and Alaska have never attempted brown trout introductions.

#### CANADA

The first introduction to North America of the Loch Leven trout occurred in 1884 when 100,000 ova were shipped from the Howietoun hatchery in Scotland to Newfoundland (Anonymous, 1887; Catt, 1950). The first of the German brown trout to reach mainland Canada came from New York State and were planted in Lac Brule, Quebec, in 1890 (Catt, 1950). A recent survey indicates that although the dissemination of brown trout in Canada was slow and dependent on neighbouring American states, all provinces but Prince Edward Island and Manitoba and the Northwest and Yukon territories ultimately experienced successful introductions. Despite naturalization in 9 of the 10 provinces, Nova Scotia and Alberta remain as the only two presently conducting stocking programs (Table III).



TABLE II. Introductions and present status of the brown trout in the United States of America.

State	Year of introduction	Survival	Current stocking programme	Naturalized distribution
Alabama	None			
Alaska	None			
Arizona	Prior to 1930	Y <sup>a</sup>	Y	Y
Arkansas	Unknown	Y	N <sup>a</sup>	Y
California	1894-95	Y	Y	Y
Colorado	1887	Y	Y	Y
Connecticut	1899	Y	Y	Y
Delaware	1950	Y	Y	N
Florida	1956-57	N	N	N
Georgia	Unknown	Y	Y	Y
Hawaii	1935	N	N	N
Idaho	1915	Y	Y	Y
Illinois	1887	Y	Y	N
Indiana	Unknown	Y	Y	N
Iowa	1885	Y	Y	Y
Kansas	1951	N	N	N
Kentucky	1948	Y	N	N
Louisiana	None			
Maine	1885	Y	Y	Y
Maryland	Unknown	Y	Y	Y
Massachusetts	1887	Y	Y	Y
Michigan	1883	Y	Y	Y
Minnesota	1888	Y	Y	Y
Mississippi	None			
Missouri	Unknown	Unknown	Y	N
Montana	1889	Y	Occasional	Y
Nebraska	1889	Y	Y	Y
Nevada	1895	Y	Y	Y
New Hampshire	1887	Y	Y	Y
New Jersey	1900	Y	Y	Y
New Mexico	1893-94	Y	Y	Y
New York	1883	Y	Y	Y
North Carolina	1887	Y	Y	Y
North Dakota	Unknown	Y	Y	N
Ohio	Unknown	N	N	N
Oklahoma	1930's	N	N	N
Oregon	Early 1900's	Y	Y	Y
Pennsylvania	1886	Y	Y	Y
Rhode Island	Late 1930's	Y	Y	Y
South Carolina	Unknown	Y	Y	Y
South Dakota	Late 1880's	Y	Y	Y
Tennessee	Unknown	Y	Y	Y
Texas	None			
Utah	1900	Y	Y	Y
Vermont	Early 1890's	Y	Y	Y
Virginia	Unknown	Y	Y	Y
Washington	1935 and earlier	Y	Y	Y
West Virginia	1925-26	Y	Y	Y
Wisconsin	1887	Y	Y	Y
Wyoming	1933	Y	Y	Y

<sup>a</sup>Y = Yes; N = no.

Quebec and Newfoundland, the first provinces to introduce the brown trout, were also the first to withdraw from major stocking programs. As of 1954, brown trout existed only as planted fish in the North River, Terrebonne





FIG. 4. Naturalized distribution of *Salmo trutta* in North America.



TABLE III. Introductions and present status of the brown trout in Canada.

Province or territory	Year of introduction	Source	Survival	Current stocking programme	Naturalized distribution
Alberta	1924	Montana	Y <sup>a</sup>	Y	Y
British Columbia	1932	Wisconsin, Montana	Y	N <sup>a</sup>	Y
Manitoba	1943	Washington	N	N	N
New Brunswick	1921	New York	Y	N	Y
Newfoundland	1884, 1892	Britain, Germany	Y	N	Y
Northwest Territories	None				
Nova Scotia	1925	Unknown	Y	Y	Y
Ontario	1913	Pennsylvania	Y	N	Y
Prince Edward Island	None				
Quebec	1890	New York	Y		
Saskatchewan	1924	Wisconsin, Montana	Y	N	Y
Yukon Territory	None				

<sup>a</sup>Y = yes; N = no.

County, and in Lake Memphremagog (Legendre, 1954). Stocking in Newfoundland was discontinued prior to the 1920's (Andrews, 1965) but the species is now widely distributed in southeastern Newfoundland especially on the Avalon Peninsula; it is also present in rivers and streams on the north side of Trinity Bay and on the Burin Peninsula. Well-established anadromous runs are also known in many of these areas. No authenticated reports are available for western or northern Newfoundland.

The Ontario Government developed an ambitious stocking program and distributed nearly 10 million fry, fingerling, and yearling brown trout to provincial waters between 1913 and 1962. Plantings were made primarily in waters marginal for the native brook trout. Distribution was discontinued after 1962 for a variety of reasons, the most important appearing to have been the low return of hatchery-reared fish realized by anglers (Mason, MS, 1961). Naturalized populations of brown trout presently occur only in river systems of southern Ontario that are tributary to lakes Huron, Erie, and Ontario.

In New Brunswick, brown trout of both Loch Leven and German origin were introduced to Saint John and Charlotte counties as early as 1921 (Catt, 1950). Catt noted, also, that excellent angling had been reported from these same waters. As well, brown trout had also been harvested in salt water off the Little Mis Pec River. Pelletier (personal communication) reports that naturalized populations now exist in the aforementioned counties.

Introductions to Saskatchewan in 1924 were primarily to the Cypress Hills region of southwest Saskatchewan. Early plantings in the Hudson Bay region were unsuccessful. The Cypress Hills plantings were continued annually



until 1934 (Wiggins, MS, 1960) and thereafter sporadically until discontinuation in the mid 1950's (Johnson, personal communication).

Nova Scotia and Alberta, the only two provinces still with stocking programs, both report widespread naturalized populations. As well, brown trout have been reported in estuarial waters off Nova Scotia (Prime, personal communication). The first introductions to Alberta's Raven River of the Red Deer system in 1924 and Carrot Creek of the Bow River system, 1925, resulted in a downstream dissemination which in the case of the latter, covered 141 km (Nelson, 1965). Plantings to date have distributed the brown trout and resulted in good angling in wide areas of the Saskatchewan and Athabaska watersheds (Paeta, personal communication).

Introductions to a few lakes of Jasper National Park, Alberta, in 1924 and 1942 were successful and resulted in natural populations. However, stocking was later discontinued and the fish poisoned, when deemed unpopular with the angler (Ward, personal communication).

In British Columbia, plantings of brown trout were made in the Cowichan and Little Qualicum River systems of Vancouver Island during the period 1932-35. Although spawning was noted in the former river system as early as 1937, natural populations made an insignificant contribution to the angler's catch (Carl et al., 1959). The practice of stocking brown trout was discontinued about 1961 (Northcote, personal communication).

In Manitoba, limited stockings between 1943 and 1961 failed to result in naturalized populations. As few stocked fish were captured by the angler, the rearing of brown trout was discontinued by 1962 (Kooyman, personal communication).

In spite of the limited naturalized distribution of the brown trout in Canada (Fig. 4), Dymond (1955) listed it and the carp *Cyprinus carpio* Linnaeus as the only two non-North American fishes in which introduction to Canadian waters proved to be significant.

#### MEXICO

Information was not obtained for brown trout in Mexico. However, rainbow trout, *Salmo gairdneri*, are endemic to the mainland at elevations of 2000-2400 m above sea level (Needham and Gard, 1959). Successful introductions of rainbow trout were reported in tributaries of the Lerma and Amoloya Rivers of the high plateaus (Berriozabal, 1937). This evidence would probably support the hypothesis that brown trout habitat does exist in Mexico.

#### PUERTO RICO

Brown trout ova were first imported to Puerto Rico around 1934. The eggs were reared to fingerlings and subsequently released in the Espiritu Santo River at El Yungue Forest. These and later introductions did not result in naturalized populations. Subsequently, stockings were discontinued by 1924 (Inigo, personal communication).



## AFRICA

## SOUTH AFRICA

The earliest importations of brown trout ova from the United Kingdom to Cape Town and Natal, South Africa, were made in 1876 (Hey, 1947). These and later importations made between 1881 and 1884 to Cape Town, King Williams Town, and the Drakensburg Mountains of Natal were failures. However, introductions of United Kingdom stock in 1890, 1892, and 1895, to cool mountain streams in the vicinity of the aforementioned areas, produced the present day naturalized populations (Smith, personal communication).

The establishment of two government hatcheries at Jonkershoek and Pirie, Cape Province, in 1893 and 1895 respectively, provided sources of brown trout for waters of the Transvaal and the Orange Free State, South Africa, and most of the nations of the south and eastern portion of the continent (Smith, personal communication; Harrison et al., 1963) (Table IV).

TABLE IV. Introductions and present status of the brown trout in Africa.

Country/province	Year		Source	Survival	Current stocking programme	Naturalized distribution
	First introduction	Successful introduction				
South Africa						
Natal	1876	1890	U.K.	Y <sup>a</sup>	Y	Y
Cape Province	1876	1892	U.K.	Y	Y	Y
Transvaal	1903	1903	Cape Prov.	Y	Y	Y
Orange Free State	Unknown	Unknown	"	Y	Y	
Basutoland (Lisotho)	1904		"			
Kenya	1906	1921	U.K.	Y	Y	Y
Malawi		1907	Cape Prov.	Y		Y
Rhodesia	1907	1929	"	Y		Y
Tanzania	1934	1934	"	Y	Y	Unknown
Uganda	1930		U.K.	N <sup>a</sup>	N	N

<sup>a</sup>Y = yes; N = no.

Smith (personal communication) reported that because of a reduction in prime brown trout habitats, the species is less abundant than in earlier years. Also, he noted that rainbow trout, *Salmo gairdneri*, introduced locally have taken over marginal waters which once supported flourishing brown trout populations. However, limited hatchery production and plantings have continued in South Africa, particularly in impounded waters. Although growth is reported to be good in ponds and reservoirs, naturalization has not occurred (Department of Nature Conservation, 1964).

## EASTERN AND CENTRAL AFRICA

All brown trout distributed in Eastern and Central Africa, except in Kenya and Uganda, although essentially of British origin, were from South African hatcheries.



The first importations were made into the waters of Basutoland (Lesotho) in 1904. Harrison et al. (1963) report that brown trout thrived and remained local to a number of large pools in the Langabeetsi, Quthing, Maseru, Sangabethu, and Mokhotlong rivers.

Successful introductions to Malawi (Nyasaland) of both brown and rainbow trout, were made in 1907 and 1908. A later importation and planting in 1932 was likely responsible for the establishment of a naturalized population in the Zomba Plateau (Harrison et al., 1963).

Rhodesia (Southern Rhodesia) attempted to introduce the brown trout in 1910, 1921, and 1924 but did not attain success until 1929 when populations were established in the streams of Inyanga, especially in regions with elevations of 1500–2300 m above sea level (Harrison et al., 1963).

Kenya experienced similar failures from 1906 and 1910 plantings but in 1921 established naturalized populations in waters of the Aberdare Mountains and Mount Kenya at minimum elevations of 2000 m above sea level (Harrison et al., 1963). Watson (personal communication) stated that the brown trout has proved less adaptable to local conditions than the introduced rainbow trout and, consequently, brown trout are now limited to about eight rivers on Mount Kenya and the Aberdare range. As well, a government trout hatchery, built in 1947, although still importing some 50,000 brown trout ova, now concentrates on annual productions of 250,000 rainbow trout ova.

Plantings of brown trout to waters of the Mount Elgon region of Uganda in 1930 failed and the project was discontinued (Semakula, personal communication). Plantings were made in streams of the Takukuya District of Tanzania (Tanganyika) in 1934 but continuous stocking has been considered necessary to maintain the species, as naturalized populations are questionable (Harrison et al., 1963).

The present naturalized distribution of brown trout in Africa (Fig. 5) is limited essentially to the rivers of mountainous regions and to eastern coastal streams of South Africa.

#### SOUTH AMERICA

##### ARGENTINA

The introduction of brown trout (*la trucha marron o europea*) to Argentina from England began as early as 1904 when plantings were made in rivers in the vicinity of Santa Cruz (de Plaza and Plaza, 1949). Since that time, the species has become naturalized in nearly all of the rivers and large lakes of the Patagonian Steepe (Mastrarrigo, personal communication) (Fig. 6).

##### CHILE

Brown trout eggs were first brought to Chile in 1905 from Hamburg, Germany, and placed in streams between 33° and 41°S lat (Astete, personal communication).

The present naturalized distribution of brown trout (Fig. 6) is more or less continuous between 30° and 42°S lat with only a few isolated populations



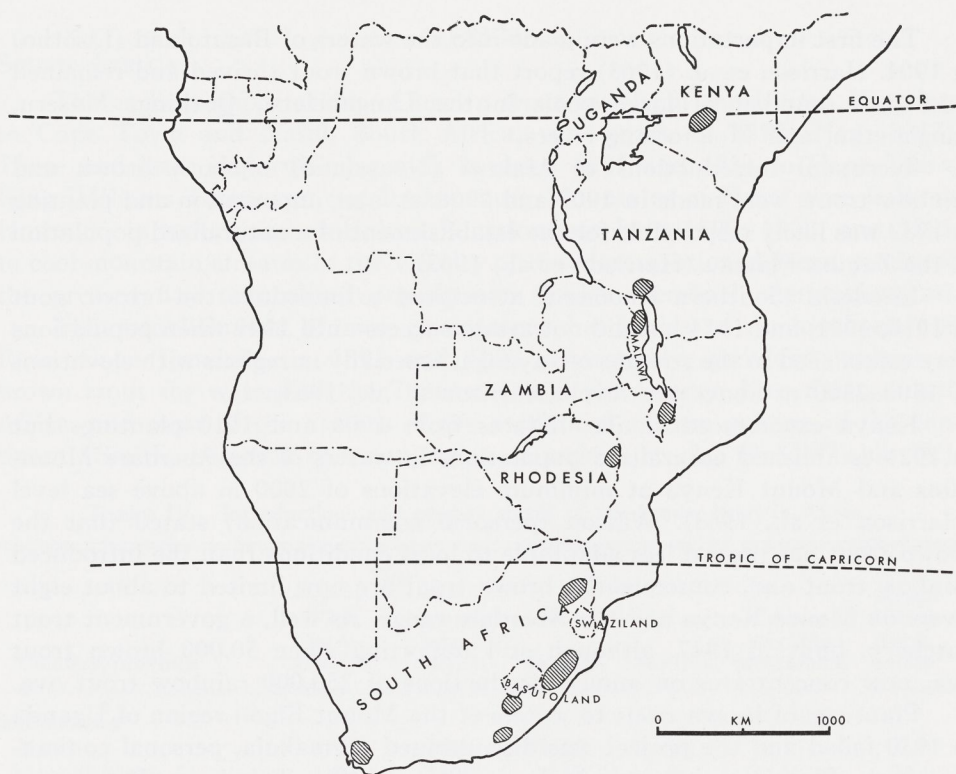


FIG. 5. Naturalized distribution of *Salmo trutta* in Africa.

beyond this range (Astete, personal communication). However, the dispersal of fish from three Government hatcheries maintains standing populations of the species between 19° and 55°S lat where the brown trout are considered to be one of Chile's richest fisheries resources.

#### PERU

Introductions of salmonids to Peru did not occur until 1928 (Tovar S., personal communication). Although the source or date of introduction of brown trout is unavailable, Tovar S. (personal communication) indicates that they are held in a trout culture station at Chucuito, State of Puno, and naturalized in the lakes and rivers of the same state at or above an elevation of 2500 m above sea level. Trout culture (although not necessarily brown trout) is also conducted in five other states encompassing elevated regions of the Andes. The hatcheries distribute trout, including the best adapted species, the rainbow trout, to the lakes and rivers of the various National Parks (Tovar S., personal communication).

Brown trout have not been introduced into Colombia where rainbow trout thrive (Gomez, personal communication). No evidence of the presence of brown trout in other countries of the Andes has been obtained. However,





FIG. 6. Naturalized distribution of *Salmo trutta* in South America.

the naturalization of rainbow trout in Ecuador in the 1930's (Howard and Godfrey, 1950) and brook trout *Salvelinus fontinalis* (Mitch.), in the Cordillera of Merida, Venezuela (Werbezahn, personal communication) supports the possibility that brown trout may be scattered throughout the length of South America.

#### THE FALKLAND ISLANDS

Although the early records of the introduction of brown trout to the Falkland Islands were lost in a fire, the first attempts at introduction were



made apparently during World War II (Arrowsmith and Pentelow, 1965). In 1947, 30,000 brown trout ova listed as *Salmo fario* were received as a gift from the Chilean Government. Most of the shipment was stocked as fry into rivers of East Falkland. From 1948 through 1952, when stocking was discontinued, 55,000 ova of lake origin were flown from Great Britain to Stanley and subsequently distributed to waters in both the East and West Falklands. Angler's returns since 1954 indicate the presence of natural reproduction and a resultant sea run population (Arrowsmith and Pentelow, 1965).

#### DISCUSSION

Dissemination of the European brown trout appears to have been so complete in the past 100 years that most areas of the world capable of supporting significant natural populations have now received introductions. Discontinuity or limitation in range is typical, however, on all continents where the species has become naturalized.

The most important ecological factor limiting the endemic geographical distribution of salmonoid fishes appears to be water temperature (Vladykov, 1963). Brett (1956) states that not only are temperature extremes important to the life of fish but also that moderate extremes may effect an inability to feed, resist diseases, reproduce successfully, and be sufficiently active in the face of competition and predation, thus causing death.

An examination of mean air temperature, which may be considered to approximate adequately water temperatures (Weatherley, 1963), reveals that mean air temperatures (Dent, 1936) not exceeding 27 C in July nor dropping below -17 C in January characterize the native range of brown trout. Further, a cold temperate climate prevails with substantial autumn and winter precipitation in the form of rain or snow.

Thermal tolerance limits for brown trout have been reported by several workers. Fry (1947) gives an upper incipient lethal temperature of between 25 and 27 C. Gardner and Leetham (1914) record the death of brown trout held at temperatures above 25 C. However, thermal requirements in the embryological stage would seem more critical than in fully developed fish. Embury (1934) gives a water temperature range of 1.9-11.2 C as that within which brown trout eggs were observed to hatch in nature. Gray (1928) states that eggs of the species can be incubated between 2.8 and 13 C and excessive mortality occurs about 15 C. Brown trout, of course, live in natural waters during cold weather at temperatures as low as 0 C.

Ferguson (1958) found that the preferred temperature of brown trout ranged between 12.4 and 17.6 C in fish living in a thermal gradient over a 2-year period. Although the optimum temperature for growth may approximate the preferred temperature, Swift (1961) reports a temperature of 12 C and Brown (1957) concludes that there are two ranges: 7-9 C and 16-19 C. Differences in thermal acclimation would seem a likely explanation for these phenomena. The ability of the brown trout, unlike many species, to exhibit peak metabolism at temperatures approaching the upper incipient lethal



temperature (Fry, 1947) would indicate that the brown trout is capable of thriving over a wide range of ambient water temperatures.

Areas of the world with naturalized brown trout populations have, as might be expected, temperature regimes similar to those of the native range. Resident populations of the species in Australia and New Zealand occur only in areas characterized by a damp temperate climate at elevations of 300 m or more above sea level. The growth rate of brown trout in New South Wales and Tasmania was found by Weatherly and Lake (1967) to exceed rates in the Lake District of England.

In South America, the naturalization of brown trout has occurred in areas typified by air temperatures reaching a maximum of 21 C in summer (January) and not exceeding 10 C in winter. The extensive elevated areas of the Cordillera of the Andes and Patagonia account for the presence of brown trout along the continental divide.

In North America, despite a wealth of native trout and char, the brown trout has become naturalized over an extensive area characterized by damp temperate to wet winter climates. The northern limit of the range follows closely a mean minimum daily air temperature in January of -12 C and a snow cover of no less than 2.5 cm extending over an annual mean maximum of 140 days. Plantings of brown trout further northward in parts of Saskatchewan and Ontario failed to establish known naturalized populations.

The southern limit of range of the brown trout in North America appears to be restricted by summer air (July) temperatures in excess of 21 C. However, range extensions into warmer areas where July temperature may reach 27 C have occurred in elevated areas of the Appalachian, Ozark, Cascade, Rocky, and Wasatch mountains. As in Africa, brown trout in North America inhabit waters in warmer regions including the Wasatch Mountains and Colorado plateau, but are limited to heights of 2000 ft or more above sea level.

Ecological factors other than temperature may be expected to limit the survival of planted fish or the establishment of naturalized populations. The absence of satisfactory spawning grounds, particularly in lowland reaches of streams where the fish have often been planted, may prevent the production of progeny especially if natural or artificial barriers prevent the upstream movement of mature fish to suitable breeding grounds. Likewise, the microhabitat may not provide the cover necessary for young or adult fish. Sporadic flooding may destroy spawning beds or microhabitat and, as in Chambe, India (Tripathi, personal communication) may completely displace the fish. Also, seasonal or permanent availability of food, predator-prey relationships, and physical and chemical factors, alone or in combination, may have significant effects on survival (Weatherly, 1963).

Although several studies have been undertaken on populations of brown trout in Great Britain (Horton, 1961; Thomas, 1964), New Zealand (Hobbs, 1948; Allen, 1951), Australia (Lake, 1957; Nicholls, 1958), and North America (McFadden and Cooper, 1962, 1964; Marshall, MS, 1968), specific differences in ecological requirements between this species and other stream-spawning salmonids are not clearly defined.



Perhaps the best evidence of ecological differences comes from the relative success of introductions of brown, brook, and rainbow trout to the waters of foreign countries. In New Zealand (Allen, 1956) where brown and rainbow trout have been disseminated to most rivers, the brown trout dominated in the South Island whereas the rainbow trout generally failed to establish itself. On the North Island, brown trout predominated to the south of a line from "Southern Hawke's Bay to north Taramaki," rainbow trout to the north of the line, and neither species was dominant along the line. Allen (1956) stated that the reason for this precise distribution was not known.

In streams of Natal, South Africa, into which brown trout were the first trout species introduced, later introductions of rainbow trout generally failed (Crass, 1964). However, Crass (1964) stated that for unknown reasons well-established populations of brown trout in the Polela River were displaced by introduced rainbow trout. In Sweden (Nilsson, 1967), plantings of brook and rainbow trout into the endemic waters of brown trout were largely unsuccessful. Similarly in France (Vivier, 1955, cited in Nilsson, 1967) attempts to acclimate brook and rainbow trout failed except in areas where brown trout were absent.

In North America, brown trout have been planted generally in waters considered to be marginal or unsuitable for native trout or char. The apparent failure of many plantings over the past eight decades to establish worthwhile naturalized populations and, as a consequence, the discontinuous distribution of the species across the continent may be attributed, in part at least, to unfavourable aquatic environments in which hatchery-reared brown trout were expected to survive and reproduce. Evidence of both the coexistence of brown trout with other salmonids and the displacement of brook and rainbow trout (Bean, 1906; Brynildson et al., 1964; Dymond, 1955) where such plantings have been made in streams, ponds, and lakes suggests that brown trout would be expected to become widely naturalized if introduced into numerous North American trout and char waters from which it has intentionally been excluded.

Any major future expansion in the world distribution of the brown trout, with the possible exception of Asia, is unlikely. Climate restrictions would seem to be of singular importance in defining the general range of the species on all continents. Because of a general disinterest in brown trout in countries which have other indigenous salmonids, and a general preference for the rainbow trout on continents where the two exotics have been established, there is no evidence of enthusiasm among fisheries managers to engage actively in further disseminating the brown trout to local waters.

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1. The first part of the paper is devoted to a general discussion of the problem of the origin of life. It is shown that the problem is one of the most important and most difficult in the history of science. It is a problem which has attracted the attention of philosophers, scientists, and the general public alike. The problem is one of the most important and most difficult in the history of science. It is a problem which has attracted the attention of philosophers, scientists, and the general public alike.

2. The second part of the paper is devoted to a discussion of the various theories which have been advanced to explain the origin of life. These theories are: (a) the theory of spontaneous generation, (b) the theory of biogenesis, (c) the theory of abiogenesis, and (d) the theory of panspermia. Each of these theories is discussed in detail, and the evidence for and against each is presented.

3. The third part of the paper is devoted to a discussion of the various experiments which have been conducted to test the various theories. These experiments are: (a) the experiment of spontaneous generation, (b) the experiment of biogenesis, (c) the experiment of abiogenesis, and (d) the experiment of panspermia. Each of these experiments is discussed in detail, and the results are presented.

4. The fourth part of the paper is devoted to a discussion of the various conclusions which have been reached by the various scientists who have studied the problem of the origin of life. These conclusions are: (a) the theory of spontaneous generation is not supported by the evidence, (b) the theory of biogenesis is supported by the evidence, (c) the theory of abiogenesis is supported by the evidence, and (d) the theory of panspermia is supported by the evidence.