SIGNIFICANCE OF MICROHABITAT SELECTION FOR FISHES IN A SIERRA FOOTHILL STREAM

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Abstract. Underwater observations were employed to map, census, and measure water velocities and vertical spatial orientations of fishes at fish locations in Deer Creek, California. Several fish species were found to spatially segregate, including rainbow trout (*Salmo gairdneri*), Sacramento suckers (*Catastomas occidentalis*), Sacramento squawfish (*Ptychocheilus grandis*) and Sacramento hardhead minnows (*Mylopharodon conocephalus*). No behavioral interactions were observed between rainbow trout and two cyprinids, Sacramento squawfish and Sacramento hardhead minnows, in stream sections where all four were present. Trout densities fluctuated independent of other species densities from early summer to fall.

Swimming endurance and metabolic rates were measured in the laboratory for hardhead minnows at various swimming velocities with the use of Brett-type respirometers. It was found that hardhead had lower scopes for activity than trout. Also, hardhead had lower metabolic rates than trout at different swimming velocities. These results imply that physiological differences between trout and hardhead can best explain their spatial segregation in the stream.

INTRODUCTION

It was believed in the past that competition between species was the major influence governing species distribution. Taft and Murphy (1950) concluded that squawfish (*Ptychocheilus grandis*) and rainbow trout (*Salmo gairdneri*) were direct competitors, though their field study was inconclusive. Dettman (1977) recorded that trout and squawfish spatially segregate in Deer Creek, each species inhabiting a different microhabitat with respect to flow rate and water depth. This evidence suggests that the assertion of Taft and Murphy needs reexamination. Reeves (1964) stated that hardhead minnows (*Mylopharodon conocephalus*) occur within the lower limits of the trout habitat "and it is probable that there is competition for food between these two species, particularly in the younger age groups." This assertion was not substantiated with data collected by Reeves, however. He failed to realize that microhabitat overlap is insufficient evidence for interspecific competition.

McNaughton and Wolf (1973) define interspecific competition as a biological interaction between two or more species which occurs when a necessary resource is in limited supply or when resource quality varies and demand is quality dependent. Resources include both food and space. Proof of interspecific competition for limited food is extremely difficult in fish communities because it is nearly impossible to accurately estimate insect densities in the stream. On the other hand, competition for space can be more easily documented because species spatial distributions can be easily measured in clear stream situations.

One objective of the present study was to measure microhabitat selection within a stream fish community. Another objective was to record any behavioral interactions which may be important in regulating habitat selection. A third objective was to examine physiological mechanisms which may also be important in determining habitat selection for suspected competitors, such as rainbow trout and hardhead minnows.

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DESCRIPTION OF STUDY AREA

Two study sites were located on Deer Creek, a low elevation, Sierran foothill stream, which flows into the Sacramento River near Vina, California. One site, in the upper canyon, was at 1500 feet in elevation and was characterized by an abundance of trout. A high ridge to the south with an additional steep wall along the immediate south shore at several points affords considerable shade for this stream section even in summer. The second study site was 15 kilometers down stream at an elevation of 500 feet. This lower canyon area was much wider with considerably less shade than the upstream section and contained low trout densities. There was a 3°C to 4°C difference in water temperature between the two areas each day.

METHODS AND MATERIALS

I. Field Study

A. Mapping of Fish Positions

Divers located fish as they swam upstream along the surface, and an assistant onshore marked the fish locations. Maps were drawn to scale of specific pools and runs. Fish locations were recorded on them according to species and numbers of individuals. Each species was number coded. Numbers of fish at each location were recorded in parentheses next to the species number (Alley, 1977). Maps were also drawn on sanded acetate sheets for mapping in the water in case an assistant was unavailable. Pencils were used on the maps because they left water resistant marks which could be erased after being transcribed to paper. The map outline was drawn with waterproof ink.

B. Fish Censusing Techniques

Counts were gathered by using underwater survey techniques. Divers searched in an upstream direction in riffles. Each observer covered a lane which was adjacent to the next observer's lane. Trout, chinook salmon juveniles and suckers (Catastomas occidentalis) were the most commonly encountered fishes in riffles and appeared to be unaware of observers until after being counted. The likelihood of counting the same trout or chinook salmon juvenile more than once within one lane was low because they were not observed to move upstream after being disturbed. Once disturbed, they usually veered off to the side or downstream. Most trout and salmon juveniles resumed their initial positions soon after the observer moved upstream. Observers notified adjacent observers of sideways movements of fish into adjacent lanes. Fish which had been disturbed and displaced by observers as they moved upstream did not hold positions and were easily distinguished from undisturbed trout. This fish behavior helped the experienced observer to avoid counting the same fishes more than once. Fish counts were accumulated on hand counters, and lane counts were added together afterwards.

Counting techniques for deeper runs were different from those used for riffles. Two observers were required to cover a deep run. Each observer floated diagonally downstream from shore to shore, covering the entire stream channel. One observer proceeded 50 to 75 feet ahead of the other. In this way the fish unseen by the first observer were seen by the latter. Fish generally swam upstream in response to an observer floating downstream. At the end of a pass, the number of fish counted of each species was compared between observers. The highest count for each species was recorded.

A third technique was used to count fish in pools. The observers started at the tail of the pool and slowly swam upstream, looking out into the pool. When two observers were available, they covered opposite sides, staying close to the shore and moving together. An observer floated back through the middle of the pool each 10 to 15 meters if the middle of the pool was unobservable from the side. Then he resumed his position near shore, even with the other diver on the opposite side. To avoid errors in counting, the independent total counts for each species were compared. However, rather than recording the highest counts as was practiced in runs, average counts were recorded instead. In pools the problem is not failure to see each fish as in the case of runs, but to avoid counting the same fish twice. During 1976 pool observations, the horizontal positions within the pools were also recorded on maps as counting progressed.

C. Measurement of Water Velocity at Fish Locations

Velocity measurements were made with a probe capable of measuring water velocities electronically. The flowmeter probe slides up and down on a calibrated staff. At each fish position the water velocity was measured by pointing the probe in the direction the fish was facing when it was in its swimming position. The flowmeter required a water temperature compensation in 1975, resulting in an adjustment when water temperature changed more than 0.5°C. Therefore, water temperatures were recorded regularly during velocity measurements. The flowmeter box, containing circuits, dials, and knobs, was positioned on a float which was 91 centimeters by 51 centimeters. The float supported two divers in deep areas of the stream, providing great maneuverability.

Fish positions were normally obtained from a downstream vantage point with the observer looking upstream at the fish. Fishes were also observed from the side and slightly downstream. The fishes appeared undisturbed from the observer's presence. Observations were never recorded from an upstream vantage point because the observer altered downstream flow patterns and disturbed normal fish behavior in such instances. The observer who made the underwater observations positioned the probe while the assistant operated the dials on the electronic box situated on the float. The assistant with float was downstream from the observer as he recorded the measurements. Total depth and fish distance from the surface were measured on the calibrated staff. Later the fish distance from the substrate was determined by subtraction.

For species which did not maintain position in the current, such as roach (*Lavinia symmetricus*), squawfish, and hardhead in some cases, water velocities and depths were measured in locations along predictable routes for each particular species. Large hardhead and squawfish maintained nearly constant vertical positions as they moved horizontally through a portion of the stream. In fast runs and slow portions of riffles, hardhead maintained positions. However, in quiet areas such as pools the hardhead as well as squawfish moved in predictable circuits. Squawfish were not seen to maintain positions anywhere. If a fish was not holding a position, the probe was positioned and directed into the current at the vertical location where the fish passed through the water column.

In quiet stream sections which lacked surface turbulence the fish were observed from onshore vantage points by individuals wearing polaroid sunglasses. The advantage of this technique is that it minimizes human disturbance. Samples were unbiased because the depth of field was normally from the water surface to the stream bottom when this technique was employed. All adult fish could be observed in these quiet areas. This technique was used to observe squawfish, suckers and hardhead minnows.

The water velocity fluctuated up and down at each fish location as the water velocity was measured. The most common velocity encountered over a 10 to 15 second interval was recorded as the representative velocity for that fish position. The range as well as the representative velocity were recorded in a number of cases to estimate water turbulence. During the summer, 1975, all velocity readings were recorded at least one hour after sunrise. Very few measurements were taken after sunset due to limited visibility, which hindered accurate measurements.

II. Laboratory Experiments

A. Fish Collection and Holding

Hardhead minnows were collected on three different occasions with beach seines in September, 1976. The fish inhabited San Antonio Creek near Angel's Camp, California. Water temperatures in the creek fluctuated from 18°C to 24°C at that time. The fish were collected shortly after dawn and transported back to the laboratory in 13°C to 15°C water. The fishes were held at the laboratory between 1 and 4 days before being placed in swimming respirometers. The majority of fish were held in tanks outside the laboratory where water temperatures ranged from 16°C to 23°C with natural light conditions. The remainder of fish were held in a tank indoors at a water temperature of 20°C with a photoperiod of 10 to 12 hours each day. Fishes were fed Gambusia until placed in respirometers.

B. Swimming Stamina and Metabolic Rate Measurements

A total of 20 hardhead minnows were exercised at 20°C ± 0.5°C, in Brett-type swimming respirometers (Brett 1964). Fishes were held in the respirometers at least 8 hours before oxygen consumption rates and tail beat frequencies were measured at various swimming velocities. After the 8 hour acclimation period, the individual fish was trained to swim against a current by avoiding an electrical field at the rear of the respirometer tube. Once the fish learned to avoid the electrical field, the field was shut off and the swimming trials began. Each swimming period lasted at least 12 minutes. The average period lasted between 15 and 16 minutes. The fishes swam continuously during each swimming period at a constant water velocity. Oxygen consumption rates and tail beat frequencies were measured at progressively faster water velocities. All fishes were forced to swim at their maximum sustained swimming velocities during their last swimming trials. Each fish was allowed to rest at least 20 minutes after each swimming period. Fish weight, standard length and total length were recorded after the last trial for each fish.

RESULTS

I. Field Study

A. Microhabitat Selection

Rainbow trout selected significantly faster water velocities than suckers, hardhead minnows, squawfish and roach. More than 50% of the trout inhabited currents with velocities between 30 and 70 cm/sec, and 20% of those measured were found swimming at velocities greater than 70 cm/sec (n = 172). There was only one fast, narrow stream section at the head of one pool in the upper canyon where trout held positions but were inaccessible to flowmeter measurements. This problem decreased measurements for trout less than one percent, perhaps depressing computed average trout velocity selection slightly below actual trout selection. In general the velocity data was unbiased by physical constraints imposed by stream morphology.

More than 60% of the suckers selected velocities between 10 and 50 cm/sec with 15% of them in currents greater than 70 cm/sec (n = 179). Suckers, in contrast to trout, stayed on the stream bottom and used little effort in maintaining position. The sucker's hydrodynamic shape apparently allowed suckers to cope with fast water velocities without expending much effort in swimming. The flowmeter probe was placed exactly where suckers grazed and measured extremely high water velocities which required suckers to swim very little to maintain position. Regarding cyprinids, 70% of the squawfish were recorded in water velocities less than 30 cm/sec (n = 92). Sixty-five percent of those hardhead measured also selected velocities less than 30 cm/sec (n = 281). The velocity selection results have included combined data from both the upper and lower canyon areas during August and September, 1975. However, average velocities selected by all four species were higher in the upper canyon than in the lower canyon (Alley 1977).

After combining total water depth measurements for both the upper and lower canyon areas, August and September, 1975, it appeared that trout and suckers selected similar depths. Forty percent of the trout (n = 172) and 50% of the suckers (n = 179) selected depths between 40 and 120 cm. In contrast, 40% of the squawfish (n = 92) were observed in water depths between 180 and 200 cm. Hardhead were more widely dispersed at depths ranging from 60 to 260 cm (n = 281).

B. Behavioral Observations

Differences in velocity and depth preferences resulted in spatial segregation of some of the species in both the upper and lower canyon study areas. In the upper canyon area, trout generally inhabited the riffles and swift heads of pools as well as the shallow tails of pools. Suckers inhabited similar areas to the trout but were beneath the trout when both species were together.

In the upper canyon the squawfish and hardhead generally inhabited the slow, deep areas of pools. No squawfish were observed in the upper canyon riffles in either 1975 or 1976. Hardhead minnows were found occasionally in slower, deeper portions of runs where some trout maintained positions during the day. No behavioral interaction was observed between hardhead and trout in these areas. The hardhead and squawfish which inhabited this upper canyon in 1975 were usually larger than the average trout. No interactions between squawfish and trout were observed.

In the warmer, lower canyon area the species distributions differed from the cooler upper canyon. In the lower canyon the rainbow trout were restricted to the riffles in August and September, 1975. No trout were seen in the pools until the middle of November when water temperatures were much reduced. However, hardhead and squawfish were much more widely distributed in the lower canyon in August and September than in the upper canyon. For example, hardhead were not only seen in deep slow areas of pools but also in the heads and tails of pools, in runs, and in slower portions of riffles. Squawfish were also present in pools, runs and riffles. Squawfish and hardhead greater than 20 cm in length behave differently. Squawfish do not hold a position in the current but spend their time cruising around. Large and small hardhead will hold positions in the current to feed on drifting insects, similar to trout behavior. We observed no intraspecific territoriality between hardhead during feeding, though, as was observed among trout.

C. Population Densities

Dramatic differences in species population densities were found when comparing the fish counts in the upper and lower canyon during the summer, 1975 (Alley 1977). Hardhead and squawfish were considerably more abundant in the lower canyon section of stream than in the upper canyon. Rainbow trout were considerably more abundant in the cooler upstream study area than in the warmer downstream area. Suckers were more abundant downstream but were also numerous upstream. During the summer, 1976, trout densities in the lower canyon were lower than the previous summer, and juvenile cyprinid and roach densities were higher in riffles of this area (Alley 1977).

II. Laboratory Experiments

A. Swimming Endurance and Metabolic Rate Measurements

As a result of the laboratory work in which hardhead minnow swimming abilities and oxygen consumption rates were measured, we were able to calculate standard metabolic rates as well as metabolic scopes for activity for a number of individuals (Alley 1977). It was discovered that when comparing hardhead with wild rainbow trout of similar weights at 20°C, hardhead had considerably lower metabolic scopes for activity (Dickson and Kramer 1971). And at a given swimming velocity, a hardhead minnow will consume less oxygen at 20°C (Alley 1977) than a rainbow trout of similar weight acclimated to 15°C (Rao 1968).

DISCUSSION

Differences in physiological characteristics between species can best explain the spatial segregation of species. No behavioral interactions were observed between trout and cyprinids. The trout occupy the stream sections of high velocities, such as riffles and heads of pools, because maximal amounts of drifting insects occur in these areas. Trout possess high food requirements due to their high metabolic rates. Consequently, it is to their advantage to inhabit these high food density areas. Trout densities are highest in riffles and heads of pools during all times of the day. They totally ignore large quiet areas of pools.

Cyprinids have the advantage over trout in warmer, slower stream sections, such as the lower Deer Creek canyon. Hardhead and presumably squawfish and roach have lower food requirements than trout. Therefore, they can survive in warmer, slower waters than trout and at greater densities than trout.

CONCLUSIONS

We may safely conclude that as stream discharge decreases and water temperatures increase, trout populations will decrease. On the other hand, cyprinid populations will increase as stream discharge decreases, as water temperatures increase and as long as deep quiet pools and runs remain. Consequently, trout densities will not diminish as long as stream discharge is sufficiently high to provide cool, deep riffles and their associated pools. Trout densities will be maintained independent of populations of squawfish and hardhead minnows.

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