AN ABSTRACT OF THE THESIS OF

Gordon H. Reeves for the degree of Doctor of Philosophy in Fisheries
presented on 27 November 1984.
Title: Interaction and Behavior of the Redside Shiner (Richardsonius balteatus) and the Steelhead Trout (Salmo gairdneri) in Western Oregon: The Influence of Water Temperature.

Signature redacted for privacy.

Abstract approved:
James D. Hall

Water temperature influenced interactions between redside shiners and juvenile steelhead trout ($\geq$1+) in the field and the laboratory. Distribution of the two species within various habitats was determined in three streams with different water temperature regimes. The range of habitats occupied by trout in allopatry at cool temperatures and at intermediate temperatures in sympatry was similar but habitats occupied by shiners in allopatry at warm temperatures and in sympatry at intermediate temperatures differed. Shiners at warm temperatures in allopatry inhabited areas of intermediate depth and high velocity, similar to those inhabited by trout in the other streams. In the presence of trout at intermediate temperatures, shiners were found in deep, slow water. Water temperature and the presence of the other species influenced production, activity, and distribution of both trout and shiners in laboratory streams. Trout dominated at cool temperatures (12-15°C) and shiners prevailed at warm temperatures (19-22°C).

The redside shiner exhibited two basic social organizations, loose aggregations and defense of an area. The type of organization observed varied with water temperature, abundance of food, and presence or absence of juvenile steelhead trout. The behavioral repertoire of the redside shiner was diverse. Size of the individual and proprietorship of an area were important in determining outcomes of interactions. Intensity of individual encounters varied with conditions in the laboratory streams. Plasticity of its social behavior appears to contribute to the ecological success of the redside shiner.

Interaction and Behavior of the Redside Shiner (*Richardsonius balteatus*) and the Steelhead Trout (*Salmo gairdneri*) in Western Oregon: The Influence of Water Temperature.

by

Gordon H. Reeves

A THESIS

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Dean of Graduate School

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INTRODUCTION

Interspecific competition between populations has been considered one of the major factors responsible for the organization and structure of natural communities. The influence of competition on the organization and structure of natural communities is being questioned at present, however. Strong (1983) and several papers in Strong et al. (1984) believe that interspecific competition is not as important a factor in community organization and structure as had been previously thought. Both works suggest that competition is important in only a few instances and that other factors, such as predation and abiotic factors, are responsible for the organization and structure of most communities. In contrast with the view of Strong (1983) and Strong et al. (1984), Schoener (1982, 1983) and Connell (1983) reviewed several studies of interspecific competition that appeared recently in selected journals. They found evidence of interspecific competition, based on different criteria, in several types of systems and between many types of organisms. The importance of competition varied within the commununity, however. Competition was most prevalent between predators and between producers and least prevalent between herbivores (Connell 1983; Schoener 1982, 1983).

Competition may vary temporally and spatially in a community, occurring only during periods when resources are scarce (Wiens 1977). Ericksson (1979) found evidence of competition for food between fish and ducks in lakes in Sweden in some years and not in others. Ducks were most abundant on lakes where fish were absent in two years but in a third year the was no difference in the abundance of ducks on lakes with and without fish. Dunham (1980) and Smith (1981) found competition between lizards in Texas and Arizona, respectively, varied between years. Effects of competition on growth and survival were greatest in dry years, when food was scarce. In wet years, when food was abundant, there was no effect of competition on either species. Connell (1983) and Schoener (1983) both acknowledge that competition may be a temporally and spatially variable.

The influence of environmental conditions on individuals has been studied extensively but has rarely been considered in competition studies. Water temperature is one of the major environmental factors that affects fish. In general, each species of fish is active over a wide range of temperatures but each functions best within an optimum range (Fry 1947). As a result of this optimum performance within a given temperature range, and within other environmental conditions, the outcome of competitive interactions between fishes may vary depending on surrounding conditions. A species that dominates under one set of conditions may not necessarily prevail when conditions differ.

The primary objectives of this study were to: (1) determine if redside shiners and juvenile steelhead trout ($\geq 1^+$) competed for space in natural streams and for food and space in laboratory streams and (2) determine the effect of water temperature on competition between the two species. The secondary objective was to describe the social behavior of the redside shiner. The latter objective was developed after work began in laboratory streams and it was apparent that the social behavior was more complex and diverse than originally thought.

The original objective of this study was to determine the effect of suspended sediment on the interactions between redside shiners and juvenile steelhead trout. Preliminary work in laboratory streams found that shiners were inactive at water temperatures that occur when suspended sediment levels in western Oregon streams are elevated. When water temperatures were increased, shiners became active and occupied the same habitat as trout. Further investigation found this to be true in field situations. As a result, the emphasis of the study was changed to examine the influence of water temperature.

Interactions Between the Redside Shiner (*Richardsonius balteatus*) and the Steelhead Trout (*Salmo gairdneri*) in Western Oregon: The Influence of Water Temperature.

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ABSTRACT

Water temperature influenced interactions between redside shiners and juvenile steelhead trout ($\geq 1^+$) in the field and the laboratory. Distribution of the two species within various habitats was determined in three streams with different water temperature regimes. The range of habitats occupied by trout in allopatry at cool temperatures and at intermediate temperatures in sympatry was similar but habitats occupied by shiners in allopatry at warm temperatures and in sympatry at intermediate temperatures differed. Shiners at warm temperatures in allopatry inhabited areas of intermediate depth and high velocity, similar to those inhabited by trout in the other streams. In the presence of trout at intermediate temperatures, shiners were found in deep, slow water. Water temperature and the presence of the other species influenced production, activity, and distribution of both trout and shiners in laboratory streams. Trout dominated at cool temperatures (12-15°C) and shiners prevailed at warm temperatures (19-22°C).

INTRODUCTION

The influence of environmental conditions has received little consideration in studies of interspecific interactions between fish or between other organisms. Several researchers have examined interspecific interactions between freshwater fish by comparing populations in sympatry and allopatry (e.g. Andrusak and Northcote 1971; Everest and Chapman 1972; Nilsson and Northcote 1981) but few have considered the influence of environmental conditions on these interactions. Sale (1979) and Connell (1980) emphasized the importance of environmental conditions when examining interspecific interactions. Two recent studies, Symons (1976) and Baltz et al. (1982), determined the effect of varying environmental conditions on competitive interactions. In the former, interactions between juvenile Atlantic salmon (Salmo salar) and various non-game species were not influenced by current velocities; Atlantic salmon dominated at all velocities presented. In the latter, the outcome of interactions between non-game species was strongly affected by water temperatures. Larkin (1956) noted that as a rule freshwater fish are adaptable to a wide range of environmental conditions and that the outcome of competitive interactions may vary depending on these conditions. A species that is dominant under one set of environmental conditions may not necessarily prevail when conditions differ.

Metabolic activity of fish and other aquatic poikilotherms is controlled by water temperature. Fish are active over a wide range of temperatures but each species functions best within an optimum range (Fry 1947). The lethal effect of temperature on fish has received much attention (e.g. Brett 1952) but sublethal effects, particularly in relation to interspecific interactions, have received little attention. Baltz et al. (1982) showed that competition between speckled dace (*Rhinichthys osculus*) and riffle sculpins (*Cottus gulosus*) for cover on riffles was mediated by water temperature. Dace dominated at warmer temperatures because they were able to function metabolically without stress while sculpins were stressed. Sculpins prevailed at cooler temperatures. Thus, water temperatures may influence the composition of fish communities by influencing not only species survival but also the outcome of competitive interactions.

There is little evidence to suggest that non-game fish successfully compete with salmonids (Flick and Webster 1975; Moyle 1977; Brown and Moyle 1981). However, a series of studies at Paul Lake, British Columbia demonstrated that introduced redside shiners (*Richardsonius balteatus*) successfully competed with rainbow trout (*Salmo gairdneri*) for food (Larkin and Smith 1954; Crossman 1959; Johannes and Larkin 1961). Little is known about the ecology of redside shiners in lotic environments, however. Rodnick (1983) found that habitats occupied by adult shiners (>25 mm total length) in an Oregon stream were similar to those utilized by juvenile steelhead trout ($\geq 1^{+}$) (Everest and Chapman 1972; Reiser and Bjornn 1979). We observed shiners and juvenile steelhead trout together in mid-order streams throughout western Oregon. Similarity of habitats utilized along with other available information suggested a strong potential for competitive interaction.

Objectives of this study were to: (1) determine if redside shiners and juvenile steelhead trout ($\geq 1^+$) competed for space in natural streams and for food and space in laboratory streams and (2) determine the effect of water temperature on competitive interactions between the two species.

MATERIALS AND METHODS

Field

Field work reported here was conducted in the Umpqua River system of central western Oregon in late July and early August, 1983 (Fig. 1). Study sites were established on three streams with different water temperature regimes and either sympatric or allopatric populations of redside shiners and juvenile steelhead trout. Physical characteristics of the sites were carefully selected for similarities. Preliminary observations leading to the selection of sites were made in a number of streams in western Oregon from 1980 to 1982 (Appendix I).

Cow Creek, a tributary of the South Umpqua River near Riddle, OR., contained redside shiners in allopatry (Fig. 1). The study area was at river kilometer 8. The Cow Creek watershed has been subjected to intensive land-use activity, primarily timber harvest, mining, and livestock grazing. Summer water temperatures reach 25°C and higher (pers. obs.). Temperatures during our observation period were lower than normal, 20 to 22°C, because of cool, overcast conditions. We observed juvenile steelhead trout and chinook salmon (*O. tshawytscha*) in Cow Creek early in the year before water temperatures increased, but no juvenile anadromous salmonids were observed by mid-June. Other species observed in the study area were sculpins (*Cottus* spp.), dace (*Rhinichthys* spp.), and juvenile Umpqua squawfish (*Ptychocheilus umpquae*).

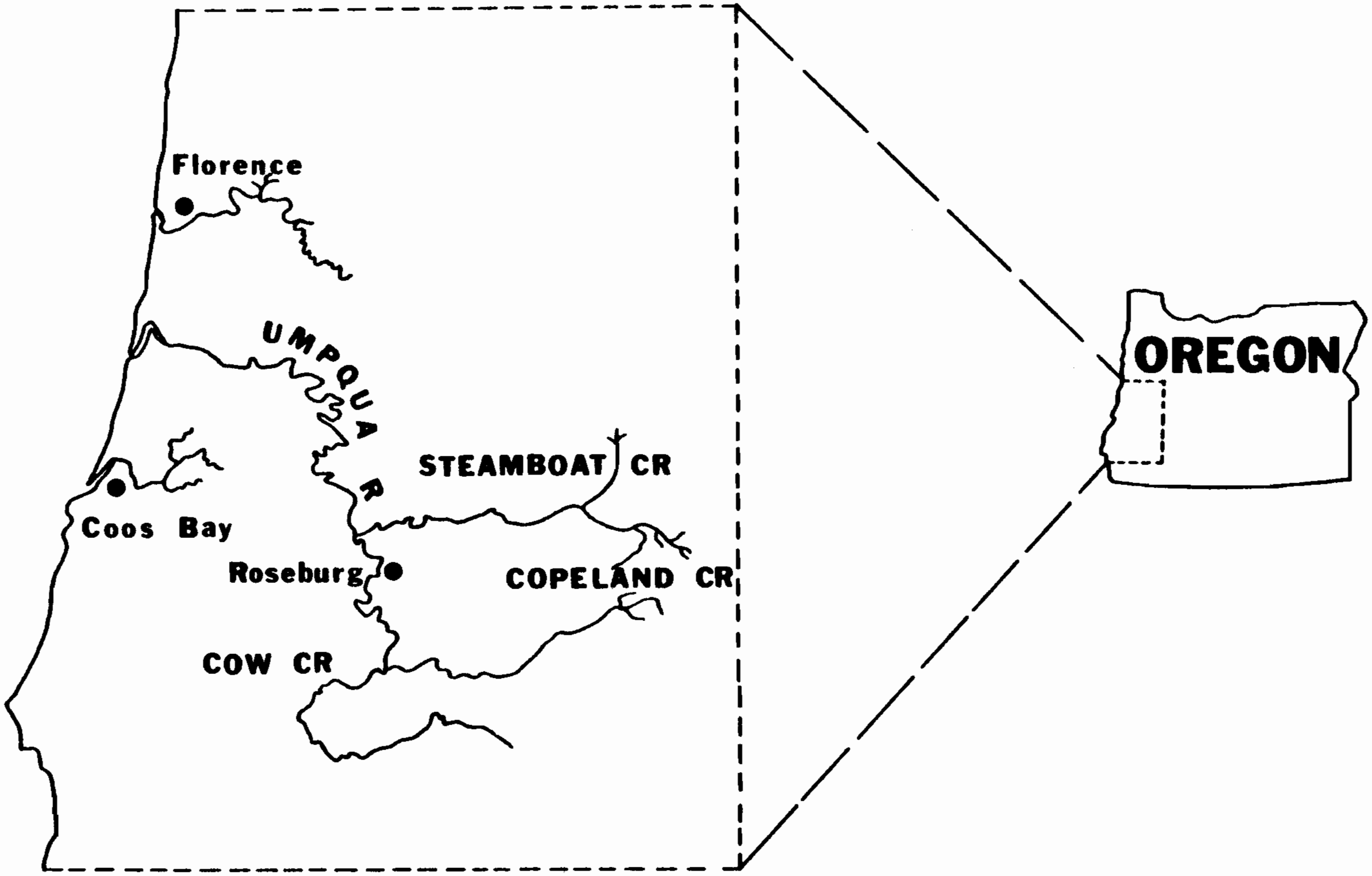


Fig. 1. Location of field sites.

The site with steelhead trout in allopatry was on Copeland Creek, a tributary of the North Umpqua River near Steamboat, OR. (Fig. 1). The study area was at river kilometer 4. Land-use activity in the watershed is limited because of steep side slopes. Summer water temperatures reach 20°C (pers. obs.) and during the study varied from 14 to 19°C. Sculpins were the only other species observed in Copeland Creek.

Both species were present in Steamboat Creek, a major tributary of the North Umpqua River 20 km downstream from Copeland Creek (Fig. 1). The study area was at river kilometer 1. Tributaries of Steamboat Creek in the past have been and continue to be logged at moderate to high levels. Water temperatures varied from 18 to 21°C during the study but normally reach 22°C in summer (pers. obs.). Other fish observed in the study area were sculpins, dace, juvenile chinook salmon, cutthroat trout (Salmo clarki), Umpqua squawfish, suckers (Catostomus spp.) and adult Pacific lamprey (Lampetra tridentata). The latter two were observed only at night.

Fish were observed by two divers using masks and snorkels. Each site was divided into 3-m squares and the corners marked with plastic flagging. Divers began at the downstream edge of a site and proceeded slowly upstream. Species, size, and location of fish were recorded on a plexiglass slate with the grid pattern of the site inscribed on it. These data were transcribed onto a map of the site at the end of an observation session. Observations were made on two consecutive days, in the morning starting between 0730-0800 h, at midday, starting between 1200-1300 h, and in the evening, starting between 1900-1930 h. Observations were also made at night using underwater lights. Because of difficulty in locating grid markers at night, only species, size, general location, and activity patterns were recorded.

Four physical factors, substrate composition, water depth, current velocity 5 cm below the surface (henceforth referred to as surface current velocity), and mean current velocity (i.e. velocity at 0.6 depth of the water column measured from the surface) were measured the day following observations on distribution. Measures were made at the corners and midpoints of each grid section, or at more frequent intervals when a factor changed significantly in a short distance. Current velocities were measured with a portable electronic current meter. Substrate composition was grouped into categories of <2 cm, 2-5 cm, 5-10 cm, 20-40 cm, and >40cm.

Distribution of each species at each time of day relative to the physical factors was determined in sympatry and allopatry with a stepwise discriminant function analysis. This procedure analyzed the distribution relative to a linear combination of all physical factors. Contours of substrate, depth, and velocity classes were drawn onto a single map. Classes of depth and velocity were at 15 cm and 15 cm sec^{-1} intervals, respectively. Substrate intervals were as described in the preceding paragraph. Intervals for each factor were assigned to a class, 1 the lowest interval, 2 the next highest, etc. Clear acetate sheets with fish locations marked on them were overlaid on a single map with contours of the classes of all physical factors. Classes of each physical variable were recorded for each fish in a homogeneous area larger than 3 m^2, which represented our level of precision. A homogeneous area was an area in which a single class of each physical factor occurred. Data from each day were combined for this analysis and separate discriminant functions were derived for each time of day that fish distribution was determined.

We also examined the distribution of each species in sympatry and in allopatry relative to each physical factor. We calculated the total area of each class and then estimated the density of fish in each class for all factors. Separate estimates were made for each time and day.

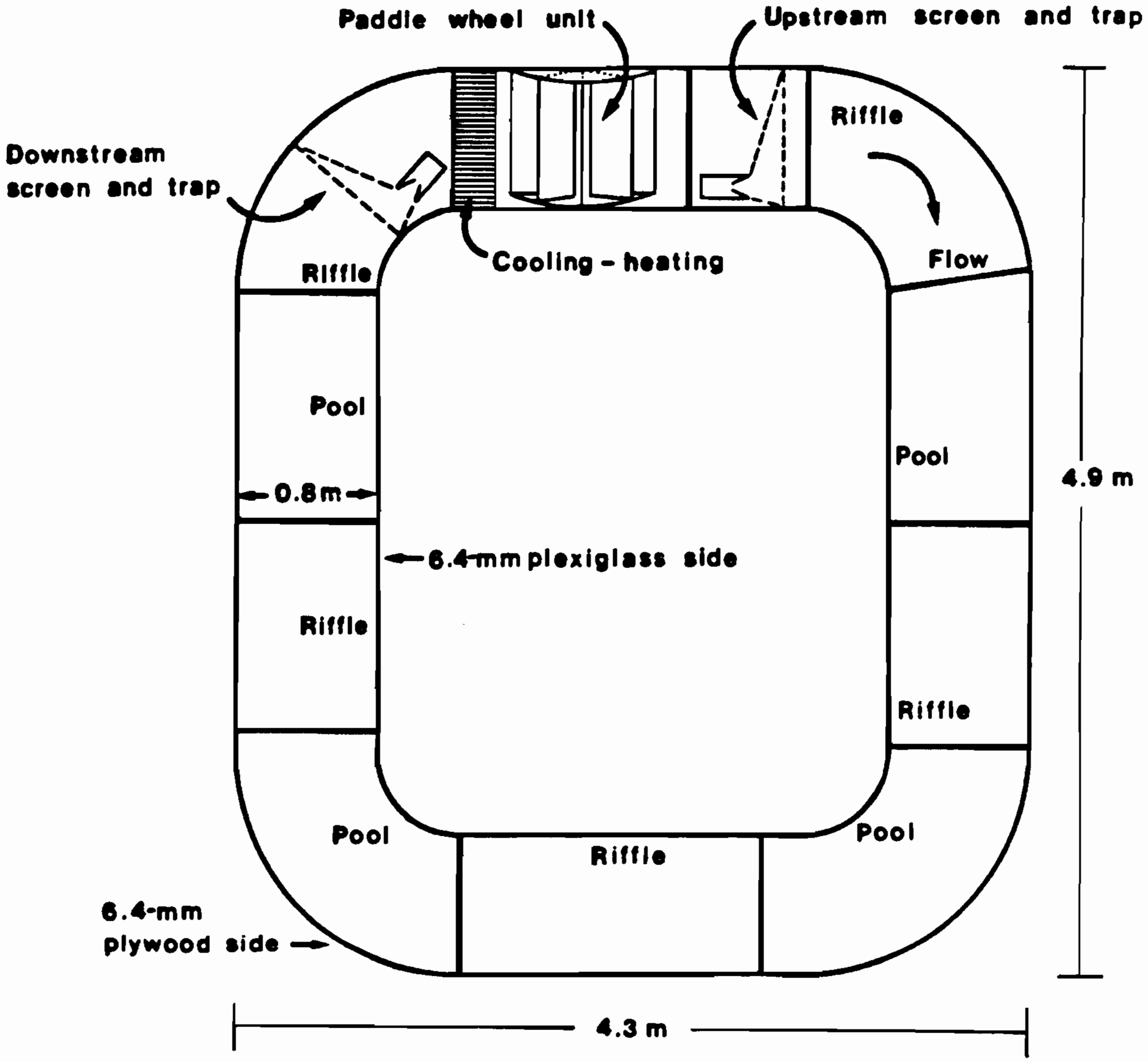
The midday observation for the first day on Steamboat Creek was excluded from analysis because eight common mergansers (Mergus merganser) were seen in the study area just before the observations. The only fish observed at that time were four dead dace that appeared to have been recently killed. Conditions appeared to have returned to normal by evening.

Laboratory

Laboratory work was conducted in a paired set of artificial stream channels located at the Forestry Sciences Laboratory, USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Corvallis, OR. Reeves et al. (1983) describe the channels in detail. Tests were conducted from June to October, 1983.

Each channel is rectangular, measuring 4.27 m x 4.87 m (Fig. 2). Channel cross-sections measure 0.76 m wide and 0.61 m deep, and each contains 5700 L of water. They are set one above the other on a metal support. The open inner portion is a viewing chamber with 6.4-mm thick plexiglass walls. Black plastic curtains suspended around the inside and outside of the channels eliminate undesired light and disturbances. The inner curtains contain observation ports at fixed intervals. Each channel has independent systems for regulating water temperature, duration and intensity of photoperiod, filtration, current velocity, and ultraviolet (UV) sterilization. Current velocity is maintained by a plexiglass paddle wheel 0.60 m in diameter. Velocity within a channel varied from 0 to 10 cm sec^{-1}. Each channel had four pools and four riffles of equal size. Depth was 50.0 cm in pools and 40.0 cm in riffles. Substrate consisted of sand and pea-gravel in pools and cobble in riffles. Cover was provided in each pool and on two of four riffles.

Tests were conducted under two daily water temperature regimes. We examined stream temperature data from U.S. Geological Survey water records for streams in western Oregon and selected temperature regimes



2. Diagram of laboratory streams.

that were representative of streams whose watersheds had been subjected to different levels of land-use. A daily temperature range from 12 to 15°C (54 to 59°F) represented systems with low levels of disturbance. Systems with greater levels of disturbance resulting from land-use practices were represented by a daily temperature range from 19 to 22°C (67 to 72°F). Temperatures in the channels were varied according to a normal diel cycle with daily lows in the morning and highs in the evening.

The photoperiod for all laboratory tests was 15 hours of light and 9 hours of darkness. The light phase consisted of a 1.5 hour "morning", where lights gradually increased from zero to full intensity, 12 hours of full intensity, and a 1.5 hour "evening", where lights gradually dimmed to zero intensity. Everest and Rodgers (1982) describe the light control used. Nine 60-watt incandescent bulbs spaced at equal intervals around the channel were the sole source of light.

Laboratory streams were filled with water 5-6 days prior to the introduction of fish. Water was from the City of Corvallis water supply and was continuously passed through a sand filter and a UV sterilizer. Make-up water was added to each channel at 0.5 L min^{-1}. Channels were drained, sterilized, and refilled between tests.

Test fish were captured by electroshocking or seining and held for 2 to 3 weeks in laboratory tanks before introduction to the channels. During this period, they were treated with malachite green to reduce chances of diseases and/or parasites, acclimated to the temperature regime to which they would be exposed, and acclimated to eat frozen brine shrimp (*Artemia spp.*).

Individual fish were weighed to the nearest 0.01 g and measured to the nearest millimeter (fork length) before introduction to the channels. Number and pattern of parr marks on steelhead trout were recorded to aid in identification of individuals during observations. Mean size (±1 SD) of trout in the various trials ranged from 95.0 mm (±9.8) and 7.2 g (±2.9) to 106.4 mm (±4.3) and 11.2 g (±0.8). Redside shiners ranged from a mean of 71.5 mm (±12.0) and 4.8 g (±2.2) to 77.2 mm (±9.9) and 5.5 g (±2.1). Number of trout in a channel at the start of a trial ranged from 4 to 6 and number of shiners from 25 to 38. Mean size and number of fish in each test are shown in Appendix II.

Test periods were 13 days. One trial with each species alone and two with both species present were run at each temperature regime. One trial with both species present was run in the lower channel and one in the upper channel. Trials with only redside shiners and only steelhead trout present are referred to as RS and SH, respectively. Trials with both species present are designated RS-SH.I and RS-SH.II.

In RS-SH trials, steelhead trout were introduced to the channels first. Traps located on the upstream and downstream side of the paddle wheel were opened after 48 hours to allow fish that were unable to obtain a suitable territory to migrate. At the end of 24 hours traps were closed and redside shiners introduced. Biomass of shiners introduced was three times the biomass of trout present at that time. This represented a relatively low ratio of shiner to trout biomass in streams where we observed the species together. We believed that if trout were affected by shiners when the ratio was low then the inference could be made that the effect would also occur at higher ratios. Traps were reopened after 24 hours and the test period began 24 hours later.

The introduction procedure in trials with a species alone varied with species. The same procedure used in RS-SH trials was followed in each SH trial. In RS trials, traps were open 24 hours after redside shiners were introduced and the test began 24 hours later. Biomass of shiners introduced in a RS trial was equal to the mean biomass used in RS-SH trials for that temperature regime.

Fish that migrated from the channels were weighed and measured as described previously. Fish that jumped out of a channel before the start of a test were replaced by similar sized individuals. After the test period began, fish that jumped out were counted as migrants. Nets were placed across the top of each channel near each trap to minimize the chances of fish leaping out.

Frozen brine shrimp, fed to the fish three times daily, were the sole food source in all laboratory tests. Daily rations were equal to 15Δ of the dry weight of salmonids present at the start of the test period. The large ration was necessary because of the poor nutritional value of the frozen shrimp. No production was found in preliminary work using daily rations of 5%, 7%, or 10%. Amount of shrimp fed in RS trials was the same proportion, relative to the initial biomass of redside shiners, fed in corresponding RS-SH trials. Fifty percent of the daily ration was presented in the morning, 25% at midday, and 25% in the evening. Food was delivered to each stream via a 2.5-cm diameter PVC pipe that ran in a zig-zag pattern along the entire area available to fish. Frozen brine shrimp were added to a box above each channel. Water was pumped to the box by the filter pump and then flowed by gravity to the feeder pipe in the channel. Individual shrimp, forced by water pressure through holes that had been drilled along the entire length of the pipe, simulated drifting insects.

Observations of distribution and behavior were made during the morning and evening feedings and before the midday feeding. During a 35-minute period, fish in each pool and each riffle, except for the most upstream riffle, were observed for 5 minutes. The number and location of fish were noted during observation of an area. Individual steelhead trout were identified whenever possible. A Wilcoxon matched pairs signed-rank test (Siegel 1956) was used to compare the number of fish observed in the upstream half with the number in the downstream half of a channel. The number of intra- and interspecific behavioral interactions was recorded. The number of redside shiners moving across a riffle was also noted. The sequence in which areas in each channel were observed was randomly determined before each observation period. The lower channel was always observed first. Viewing the most upstream riffle in either channel was difficult because of the location of the feeding boxes. Only numbers and locations of fish were noted there. Light cycles were staggered by 45 minutes so that each channel could be observed under similar light conditions.

The procedure used to estimate production, defined as the total amount of new tissue elaborated during the test period, varied depending on whether all individuals of a species could be accounted for or not. Fish remaining in the channels at the end of a test period were removed, weighed, and measured. When all individuals were recovered, production was calculated as the difference between the beginning and ending biomass of the species. Ending biomass included fish that remained in the channel for the duration of the trial and fish that migrated during the trial.

A different estimation procedure was used when we could not account for all fish. We identified the unrecovered individuals by comparing the length and weight of fish that were introduced into a channel with the length and weight of fish that remained in a channel for the duration or migrated. When we could not identify an individual, we identified the size group to which the unrecovered individual probably belonged and assumed that the individual was of mean size of that group. The mean rate of change in weight per day for the population was determined using residents and migrants. We assumed that unrecovered fish lived for half the test period and either gained or lost weight at the same rate as the population.

Weight of unrecovered fish was estimated to be the sum of the initial weight plus or minus the estimated change. The sum of the estimated weight of unrecovered fish was added to the biomass of migrants and fish that remained in the channel. Production was the difference between this sum and the total initial biomass. We accounted for all steelhead trout except for one individual in the RS-SH.I trial at warm water temperatures. We could account for all redside shiners in only the cold RS trial. Two shiners, or from 5 to 6% of the total number of shiners, were unaccounted for in each of the other trials.

RESULTS

Field

Distribution patterns and habitat preferences of both species were similar in allopatry (Fig. 3). Both species were distributed across the entire range of a given habitat feature with few exceptions. Modes for each feature were at or close to the same value for each species. There was little change in distribution over the course of the day except that redside shiners shifted from small substrate (2-5 cm) in the morning (Fig. 3A) to intermediate size (10-20 cm) at midday (Fig. 3B) and to the largest category (>40 cm) by evening (Fig. 3C).

Distribution patterns of steelhead trout were similar in sympatry and allopatry (Fig. 3). The exception was that few trout were observed in shallow water ($\leq$30 cm) or areas with small substrate (<5 cm) in sympatry, whereas fish were found in these areas in allopatry.

Habitat utilization by redside shiners was more restricted in sympatry than in allopatry. Patterns of habitat use by shiners in allopatry were characterized by broad occupancy of a variety of habitats at all times of the day (Fig. 3). In sympatry, all shiners observed in the morning were in deep water ($\geq$76 cm) over large substrate (>20 cm) and in slow to intermediate mean current velocities ($\leq$30 cm sec^{-1}) (Fig. 3A). Fish were found over a greater range of categories at midday, especially with regard to

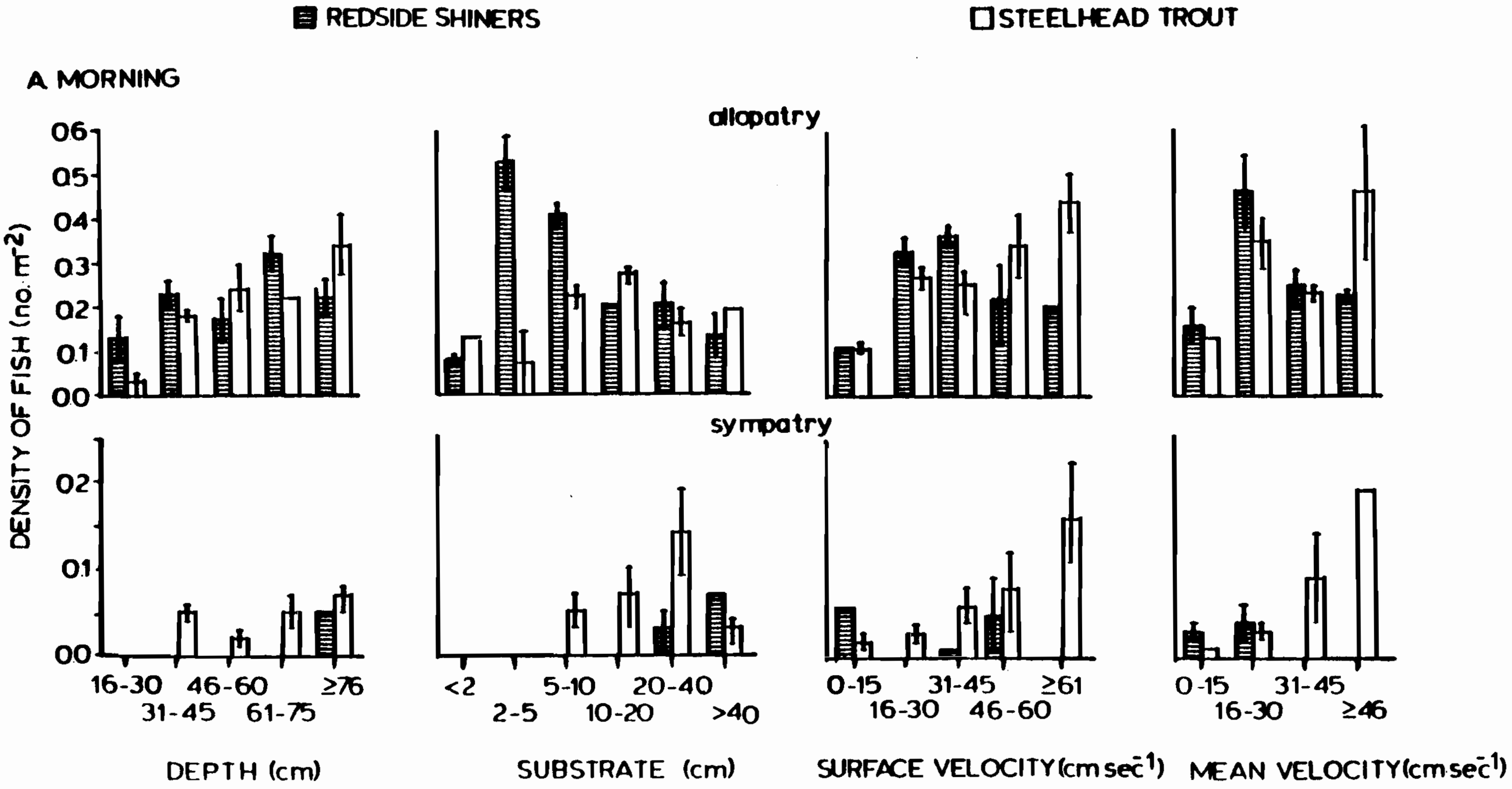


Fig. 3. Mean density of redside shiners and juvenile steelhead trout in sympatry and allopatry at different times of day in relation to physical features of study sites. Vertical bars represent range. Midday observations in sympatry were only made on one day. Note difference in scales between sympatry and allopatry.

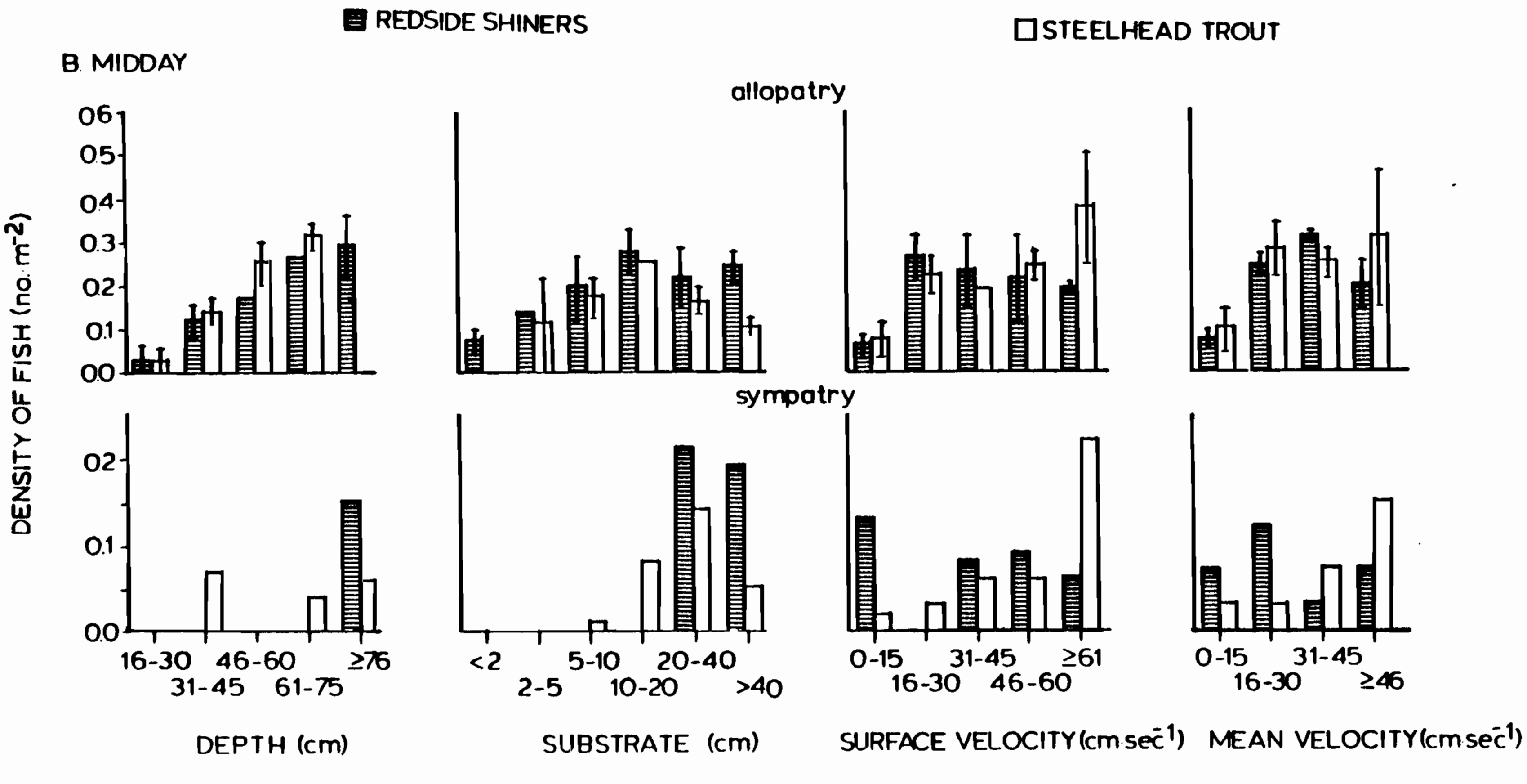


Fig. 3. (continued)

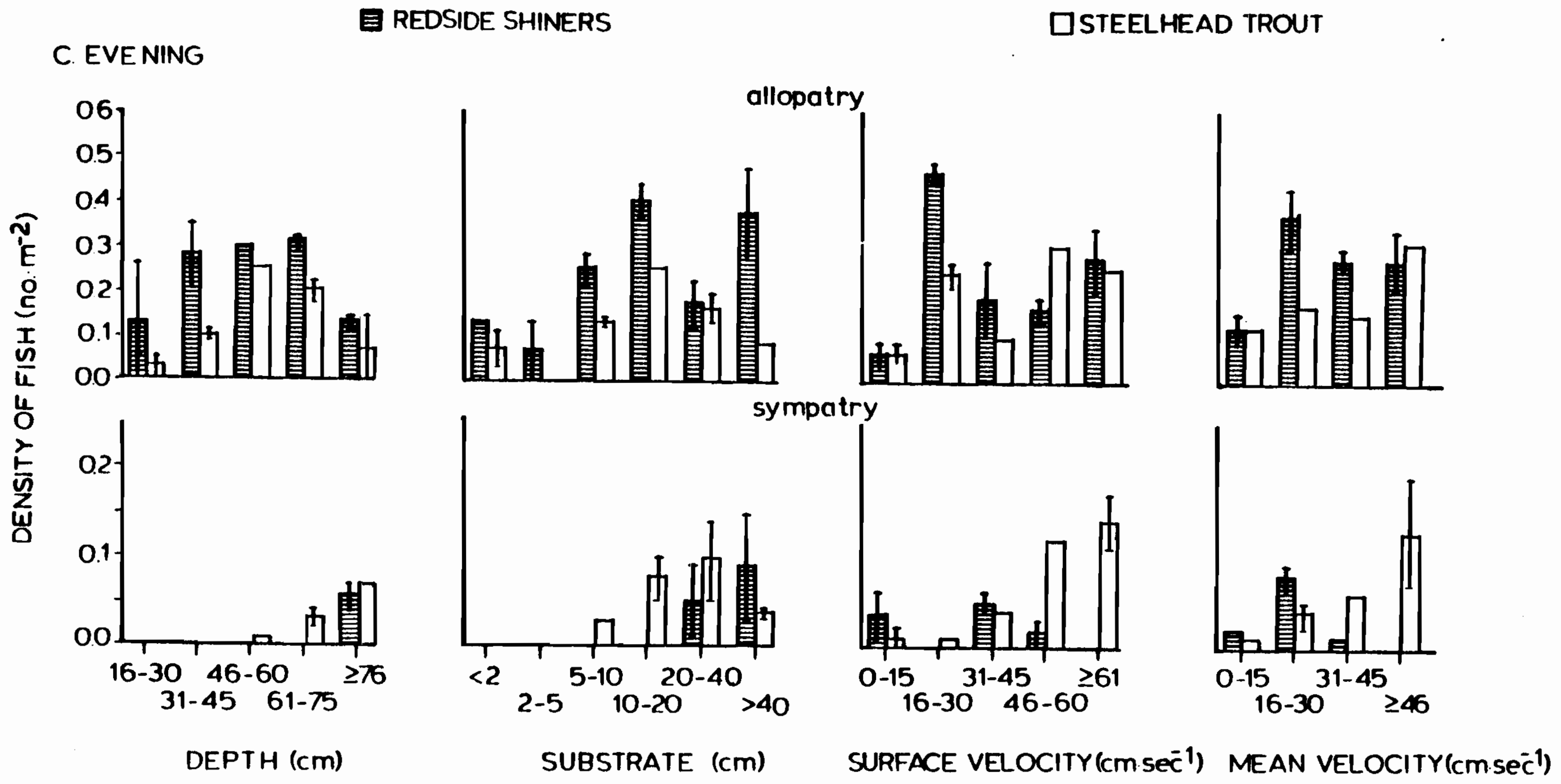


Fig. 3. (continued)

current velocities (Fig. 3B). Distribution patterns in evening were more restricted (Fig. 3C), resembling morning patterns.

For each time of day, a single discriminant function accounted for a large percentage of observed variation in habitats occupied in the three streams. Each derived discriminant function had a highly significant Wilks' λ ($P<0.001$), which is a measure of the function's discriminating power. The discriminant function for the morning accounted for 83.2% of the variation among the groups, which were each species in allopatry and sympatry. Depth, substrate, and mean current velocity were the dominant variables. The former two were positively correlated ($P<0.01$) with the discriminant scores, and the latter was negatively correlated ($P<0.05$) with the discriminant scores (Table 1). The discriminant function for midday accounted for 85.4% of the among group variation. All physical factors were highly significantly correlated ($P<0.01$) with the discriminant scores (Table 1). Depth and substrate were positively correlated and velocity measures negatively correlated with the discriminant scores. The discriminant function for the evening accounted for 84.2% of the among group variation. Depth and substrate were positively correlated ($P<0.01$) and mean current velocity negatively correlated ($P<0.05$). with the discriminant scores (Table 1).

The measured physical characteristics of the three streams in which fish were observed did not differ statistically ($P>0.05$). Two discriminant functions derived from a step-wise discriminant

Table 1. Correlation between discriminant scores derived from a stepwise discriminant function analysis and physical factors at each time of day. N is number of fish observed.

Time	Physical factor	r	significance
Morning	depth	0.683	<0.01
(N = 125)	substrate	0.702	<0.01
	mean current velocity	-0.194	<0.05
	surface current velocity	-0.094	>0.05
Midday	depth	0.519	<0.01
(N = 141)	substrate	0.487	<0.01
	mean current velocity	-0.249	<0.01
	surface current velocity	-0.290	<0.01
Evening	depth	0.741	<0.01
(N = 135)	substrate	0.626	<0.01
	mean current velocity	-0.195	<0.01
	surface current velocity	-0.134	>0.05

function analysis had highly significant Wilks' λ's ($P<0.001$). A pair-wise comparison of the centroids found no significant difference ($P>0.05$) between any of the streams.

Discriminant function analysis allowed determination of the habitats used at each time of day by each species in sympatry and allopatry when all physical factors were considered together. All possible pairs of the mean discriminant score of each group were compared by a t-test to determine if the means were statistically different (Table 2). The mean, 95% confidence limits, and 95% tolerance limits (Guttman 1970) of each group's discriminant scores at different times of the day are shown in Fig. 4. In this instance tolerance limits represent the range of locations, as determined by discriminant analysis, in which 95% of a group is inferred to occur. They provide a method to examine the range and extent of overlap of the habitats occupied by each group. The greater the overlap of the tolerance limits the greater the overlap or similarity of habitats utilized.

In the morning, there was no difference ($P>0.05$) between mean scores of redside shiners and steelhead trout in allopatry, and the tolerance limits overlapped broadly. However, shiners were observed in much a narrower range of habitats than were trout (Fig. 4A). The mean score of each species in allopatry was different from the mean score of that species in sympatry but the extent of overlap of the tolerance limits varied. The mean scores of trout in sympatry and allopatry differed ($P<0.01$) but there was extensive overlap of the

Table 2. Pair-wise comparison of the mean discriminant scores of each species in allopatry and sympatry at different times of the day.

	t	Significance	df
Morning			
Steelhead trout allopatry			
Steelhead trout sympatry	2.257	<0.01	72
Redside shiners allopatry	1.440	>0.05	92
Redside shiners sympatry	12.42	<0.001	58
Steelhead trout sympatry			
Redside shiners allopatry	4.77	<0.001	73
Redside shiners sympatry	11.25	<0.001	39
Redside shiners allopatry			
Redside shiners sympatry	14.92	<0.001	60
Midday			
Steelhead trout allopatry			
Steelhead trout sympatry	3.741	<0.001	56
Redside shiners allopatry	1.317	>0.05	107
Redside shiners sympatry	14.06	<0.001	58
Steelhead trout sympatry			
Redside shiners allopatry	6.896	<0.001	79
Redside shiners sympatry	7.571	<0.001	30
Redside shiners allopatry			
Redside shiners sympatry	14.45	<0.001	83
Evening			
Steelhead trout allopatry			
Steelhead trout sympatry	7.451	<0.001	63
Redside shiners allopatry	1.045	>0.05	120
Redside shiners sympatry	16.89	<0.001	56
Steelhead trout sympatry			
Redside shiners allopatry	9.464	<0.001	101
Redside shiners sympatry	8.205	<0.001	37
Redside shiners allopatry			
Redside shiners sympatry	21.24	<0.001	94

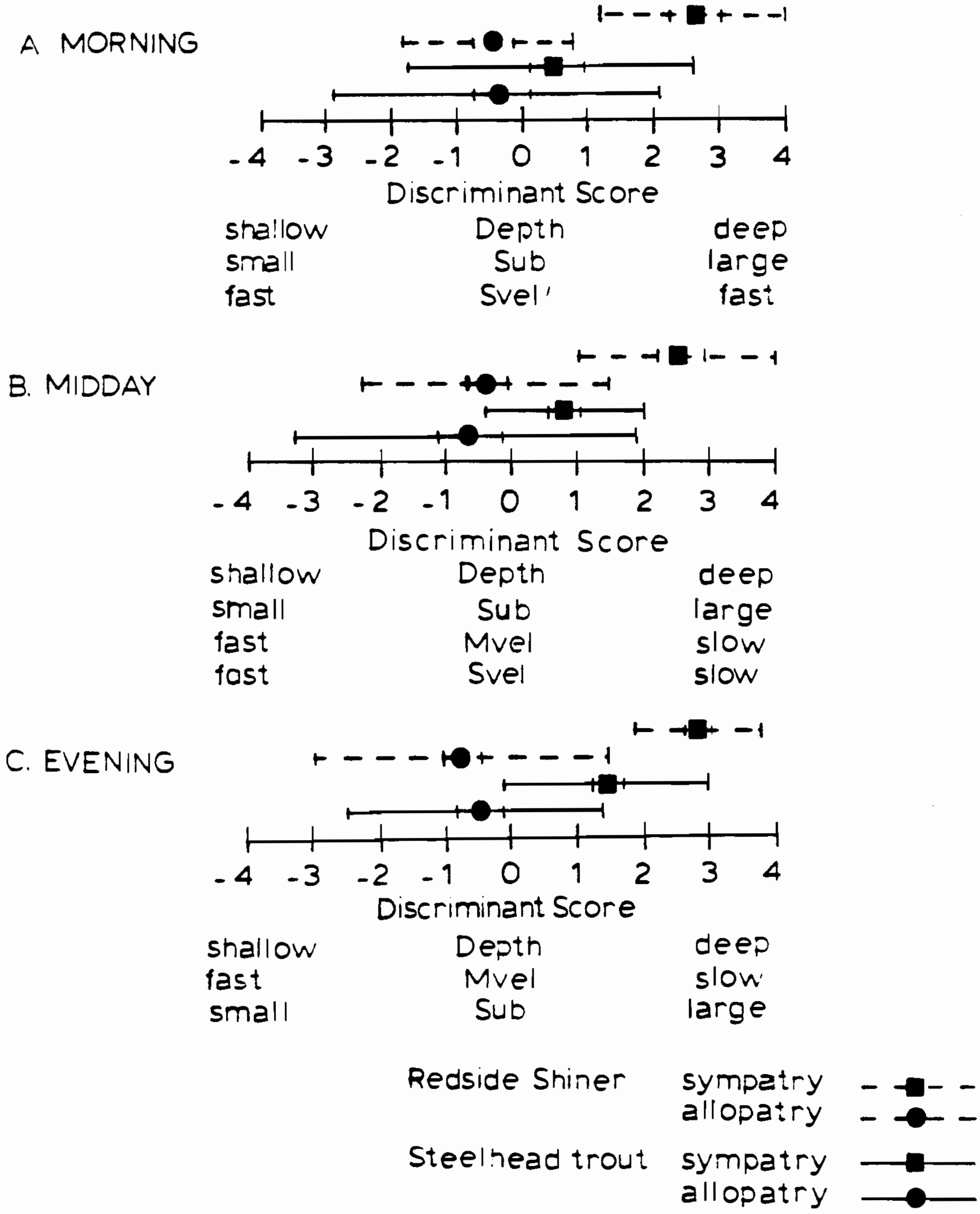


Fig. 4. Mean discriminant score, 95% confidence interval (inner brackets), and 95% tolerance interval (outer brackets) for each species in sympatry and allopatry at different times of day. Only physical factors that are significantly correlated (P<0.05) with the discriminant score are shown. Factors are shown in the order they entered into the discriminant function.

tolerance limits. This overlap indicates that trout in both situations used a wide range of similar habitats despite the statistical difference between mean scores of the two groups. Trout in both situations primarily utilized areas 31-75 cm deep, with intermediate sized substrate, and with intermediate to fast current velocity (Fig. 3A). In the morning, the mean scores of shiners in sympatry and allopatry also differed ($P<0.01$), but the tolerance limits did not overlap (Fig. 4A).

In sympatry, habitats utilized by each species in the morning also differed ($P<0.01$), but there was some overlap of the tolerance limits (Fig. 4A). Redside shiner distribution was reduced compared to steelhead trout (Fig. 4A). Shiners were restricted to deep areas with large boulders and bedrock substrate and slow mean current velocity (Fig. 3A). Trout were observed over a much wider range of each physical feature (Fig. 3A). While shiners and trout were observed in similar areas, there were noticeable differences in their behaviors and activity levels. Most shiners observed in sympatry were inactive, holding near the substrate behind large rocks or in crevices between rocks. During the same period, trout in sympatry moved throughout the water column and actively fed on objects carried by the current. Trout in allopatry and shiners in allopatry exhibited the same type of activity pattern.

At midday, the same pattern of differences between mean scores of the groups that occurred in the morning was observed. There was no difference ($P>0.05$) between means of redside shiners and steelhead trout in allopatry and the tolerance limits overlapped broadly. The range of habitats in which shiners in allopatry were observed was greater at midday than in the morning (Fig. 4B). In sympatry, the mean scores of trout and shiners were different ($P<0.01$) (Table 2) but there was some overlap of the 95% tolerance limits (Fig. 4B). Mean scores of each species in allopatry also differred from mean scores of each species in sympatry ($P<0.01$). Tolerance limits of the trout overlapped much more than did those of the shiners, however (Fig. 4B). Distribution of trout in sympatry was restricted at midday relative to the morning. This change in distribution appeared to be due primarily to the fact that no trout were observed in water 46-60 cm deep (Fig. 3B). Trout in sympatry and allopatry were less active at midday than they were in the morning; they held a position and made few movements, either vertically or horizontally. Habitat distributions of shiners overlapped slightly at midday (Fig. 4B). Shiners in allopatry generally inhabited shallower areas with greater current velocities than shiners in sympatry (Fig. 3B). Shiners in sympatry were observed, as in the morning, in deeper areas with large substrate (Fig. 3B) but they moved to areas of higher current velocities (Fig. 3B) and were more active at midday than they had been in the morning, moving throughout the water column to capture items in the drift. At this time shiners that moved into the vicinity of the trout were seldom harassed.

In the evening, the same pattern of differences between groups that occurred in the morning and midday was observed. In allopatry, there was no difference ($P>0.05$) between the mean scores of redside shiners and steelhead trout (Table 2) and there was almost complete overlap of the tolerance limits. Shiners were observed in a wider range of habitats than at any other time of the day, while the range of habitats utilized by trout decreased (Fig. 4C). As at other times, there were differences between the mean scores of each species in sympatry and allopatry ($P<0.01$). Tolerance limits of the trout continued to overlap broadly but the amount of overlap, relative to other times of the day, decreased. This decrease was due to a shift in trout distribution in sympatry to areas of deeper water and large substrate (Fig. 3C) and to a decrease in the range of habitats occupied by trout in allopatry relative to other times of the day (Fig. 4C).

In sympatry, the mean scores of each species were different in the evening ($P<0.01$) (Table 2) but there was large overlap of the 95Δ tolerance limits (Fig. 4C). Shiner distribution in sympatry was more restricted in the evening than at any other time of the day. Shiners were observed primarily in the deepest areas and in slow mean current velocities (Fig. 3C). Trout were observed primarily in deeper water also but they were in areas of higher current velocities (Fig. 3C). When the two species were observed in the same area, redside shiners were in small groups of 3-4 fish and generally held behind large rocks and boulders and would dart into the water column in an attempt to capture items carried in the current. Shiners that attempted to move into or through areas occupied by trout were quickly driven away.

In addition to differences in habitats utilized by redside shiners in allopatry and sympatry at all times of the day, there were differences in the social behavior and organization of shiners in the two situations. Shiners in sympatry were in small groups and exhibited no antagonistic behavior toward each other. In allopatry, shiners were more dispersed and there were many intraspecific interactions observed.

At night, steelhead trout in sympatry and allopatry were observed in the same general habitats and exhibited similar behaviors. Fish drifted downstream and to stream margins as light levels decreased. After dark, fish were found primarily in areas 30-60 cm deep, with 5-20 cm substrate, and with little or no current. They were on the substrate or in crevices in the substrate and showed no signs of activity, generally not moving unless a diver attempted to touch them. Large organic debris was also used for cover by some fish.

Redside shiners in sympatry and allopatry were observed at night in habitats similar to those described above as occupied by steelhead trout but there were differences in activity levels. Shiners in allopatry behaved the same as trout. Shiners in sympatry were more active than those in allopatry; they were observed swimming about, actively picking at the substrate and then spitting out material, but we could not tell conclusively if they were feeding. There were often large numbers of shiners in a given area but no behavioral interactions between individuals were noted. Trout in the vicinity were never observed reacting to shiners. By first light, no shiners were observed in these areas of Steamboat Creek; they were only observed in the deeper, slower areas described previously. Trout had also moved away from stream margins by this time.

Laboratory

Water temperature influenced production, activity levels, distribution of each species in laboratory streams, and the effect of one species on the other. Steelhead trout fared better at cool temperatures when alone and had a greater impact on redside shiners than shiners had on trout at cool temperatures. Shiners fared better at warm temperatures when alone and dominated interspecfic trials at warm temperatures.

Production

Production by steelhead trout, when alone, was 2.4 times greater at cool water temperatures than at warm temperatures (Table 3). The number and biomass of trout were greater in the cool channel than the warm channel throughout the test period. At the start of the test period, there were six fish in the cool channel, total biomass 47 g ($\bar{X}$ = 7.9 g ± 2.2) and four in the warm channel, total biomass 29 g ($\bar{X}$ = 7.2 g ±1.5). There were always more fish and a greater biomass of trout in the cold channel than the warm channel (Appendix II). Four fish remained in the cool channel for the duration of the test and three in the warm channel. Weight gains by individuals of all social status were greater at cool temperatures than at warm temperatures (Table 4). The dominant individual and subordinates gained 1.4 and 4.0 times more weight, respectively, at cool temperatures than their warm water counterparts. There was little difference in weight change by migrants in the two temperature regimes. There was no sign of infection with *Flexibacter columnaris* in migrants from either temperature. However, one resident trout in the warm channel was infected with *F. columnaris*, and was in poor physical condition.

Production by redside shiners, when alone, was 1.5 times greater in warm water than cool water (Table 3). At the start of the test period, there were nearly equal numbers and biomass of fish in each

Table 3. Total production (g) by redside shiners and juvenile steelhead trout when the species were alone and together at different water temperatures in laboratory streams. Trials with only redside shiners and only steelhead trout present are referred to as RS and SH, respecitively. Trials with both species present are designated RS-SH.

Trial	Temperature (°C)	Production (g)	
		Steelhead trout	Redside shiner
SH	12-15	9.0	--
	19-22	3.7[a]	--
RS	12-15	--	6.3
	19-22	--	9.4[b]
RS-SH	12-15	I. 9.0	I. -1.1[b]
		II. 9.1	II. -4.9[b]
RS-SH	19-22	I. 2.3[b]	I. 9.3[b]
		II. 1.1	II. 9.2[b]

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[a] Does not include weight change, -1.7 g, of one fish that was determined after completion of trial to be either a resident rainbow trout (*Salmo gairdneri*) or a precocious steelhead trout.

[b] Estimate adjusted to include calculated production of unrecovered fish.

Table 4. Social status and mean weight change (g) of steehead trout at different water temperatures in laboratory streams with redside shiners present or absent. Number of fish and range of weight changes in parentheses.

Social		Trial		
Status	Cold SH	Warm SH	Cold RS-SH	Warm RS-SH
Dominant	4.3 (1)	3.2 (1)	I. 3.2 (1) II. 3.0 (1)	I. 2.9 (1) II. 1.3 (1)
Subordinate	1.5 (3) (0.1 - 2.2)	0.4 (2) (0.0 - 0.7)	I. 1.6 (4) (0.1 - 2.5) II. 1.5 (3) (-0.4 - 2.6)	I. -- (0) II. -- (0)
Migrant	0.1 (2) (0.0 - 0.2)	-0.3 (1)	I. -0.6 (1) II. 1.6 (1)	I.-0.2 (3) (-0.9 - 1.0) II.-0.1 (2) (-0.5 - 0.4)
Total Production (g)	9.1	3.7[a]	I. 9.0 II. 9.1	I. 2.3[b] II. 1.1

[a] Does not include weight change, -1.7 g, of one fish that was determined after completion of trial to be either a resident rainbow trout or a precocious steelhead trout.

[b] Estimate adjusted to include calculated production of one unrecovered fish.

channel: 27 fish in the warm channel with a total biomass of 149 g ($\bar{X}$ = 5.5 g ±2.1); 28 fish in the cool channel, total biomass 154 g ($\bar{X}$ = 5.5 g ±2.0). No shiners migrated from the cool channel but 8 (30% of the total) left the warm channel. Migrants were generally larger individuals, ($\bar{X}$ = 6.6 g ±1.9). Fish left the channel through day 13 of the trial (Appendix II). Four of the migrants were infected with *Flexibacter columnaris* and in poor physical condition. No obvious pattern of migration was noted; fish migrated via both upstream and downstream traps and at all times of day.

At cool water temperatures, production by trout in the presence of shiners was equal to production by trout when alone (Table 3). Production by dominant trout was reduced, relative to the dominant trout in the cool SH trial but mean production by subordinates was about equal (Table 4).

Presence of steelhead trout at cool water temperatures had a pronounced effect on redside shiners. Total production by shiners was negative in both trials when trout were present, mean -3.0 g (Table 3). Production was 6.3 g when shiners were alone. At cool temperatures, number and condition of migrant redside shiners differed in the presence or absence of steelhead trout. No shiners migrated from the channel when they were alone but in the presence of trout 26% (10/38) and 20% (7/35) of the shiners left the channels in RS-SH.I and II, respectively. Migrants in RS-SH.I were slightly smaller ($\bar{X}$ = 4.3 g ±0.9) than fish that remained in the channel ($\bar{X}$ = 4.8 g ±1.4), but the opposite was true in RS-SH.II where migrants averaged 6.7 g (±2.0) and residents 5.2 g (±2.2). Individuals migrated primarily at night over the course of the study period, with about equal numbers leaving via the upstream and downstream traps. Over 50% of the migrant shiners were infected with F. columnaris and in poor physical condition.

Redside shiners had a strong impact on steelhead trout at warm water temperatures. Production by trout decreased by an average of 54%, relative to when trout were alone (Table 3). Only one trout was able to successfully maintain a territory and remain in the channel in each trial. All other trout migrated 1-3 days after the shiners were introduced and, on the average, lost a small amount of weight before leaving the channel (Table 4). These individuals attempted to maintain a suitable territory prior to leaving but appeared to be overwhelmed by the number and activity levels of shiners. Four of the five migrant trout were infected with F. columnaris. Migrants averaged 7.7 g (±2.8) and 10.1 g (±5.0) in RS-SH.I and II, respectively, compared to 8.7 g (±1.5) in the warm trial when shiners were absent. The single fish that remained in each trial was a smaller sized individual, 7.6 g in RS-SH.I and 6.5 g in RS-SH.II. The larger of these two trout fared better than the smaller (Table 4).

Total production by redside shiners in warm water did not differ when steelhead trout were present and absent (Table 3). The percentage of redside shiners migrating from the channels at warm temperatures in the presence of trout (21%) was smaller than when shiners were alone (30%). Migrants in RS-SH.I were smaller ($\bar{X}$ = 5.2 g $\pm$1.4) than fish that remained in the channel ($\bar{X}$ = 5.5 g $\pm$1.4). Migrant shiners in RS-SH.II were larger, ($\bar{X}$ = 6.9 g $\pm$1.6), than fish that remained in the channel ($\bar{X}$ = 6.3 g $\pm$2.7). Over 75% of the migrants in the RS-SH tests were infected with F. columnaris as compared to 50% in the warm RS trial and 50% in RS-SH trials at cool temperatures.

Activity

The type and number of behavioral interactions between steelhead trout were not affected by water temperature when they were alone. There were no significant differences (ANOVA $P>0.05$) between the number of interactions per fish per observation period at any time in the two temperature regimes (Fig. 5). Nips and chases (Hartman 1965) were the dominant types of interactions observed.

Interactions between redside shiners were influenced by water temperature when shiners were alone. There were significantly more behavioral interactions per individual per observation period (ANOVA $P<0.05$) at all times of day at warm temperatures (Fig. 5). Dominant types of behavior were nips in the warm stream and evictions (Reeves et al. in prep.) in the cool stream.

At cool temperatures, number of interactions per steelhead trout per observation period varied between trials and time of day (Fig. 5). The greatest number of interactions was observed during feeding periods. Trout initiated more interactions in RS-SH.II than

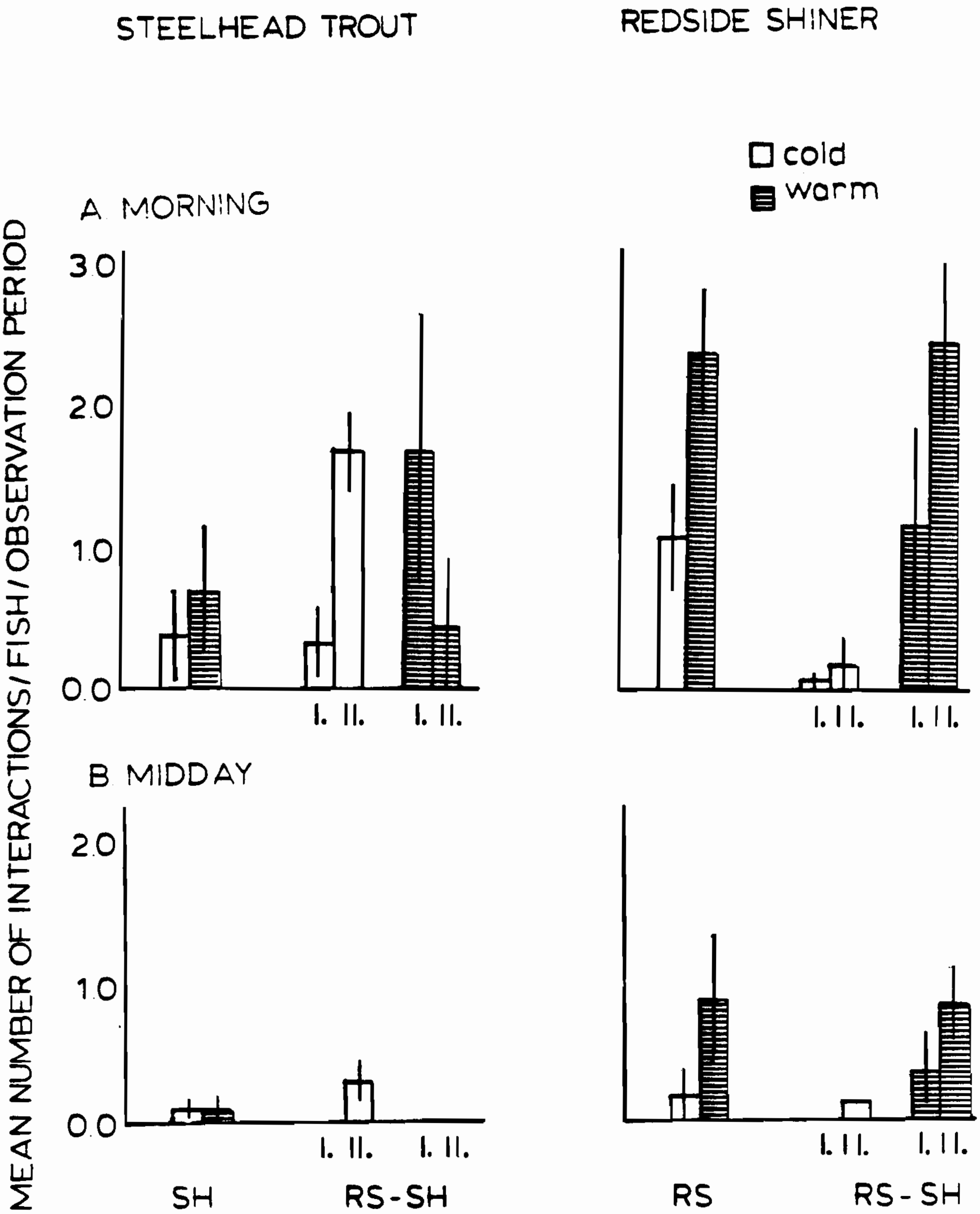

Fig. 5. Mean number of interactions per fish per observation period (5 min) for each species when species were alone and together at different water temperatures in laboratory streams. Vertical bars represent ±2 SE.

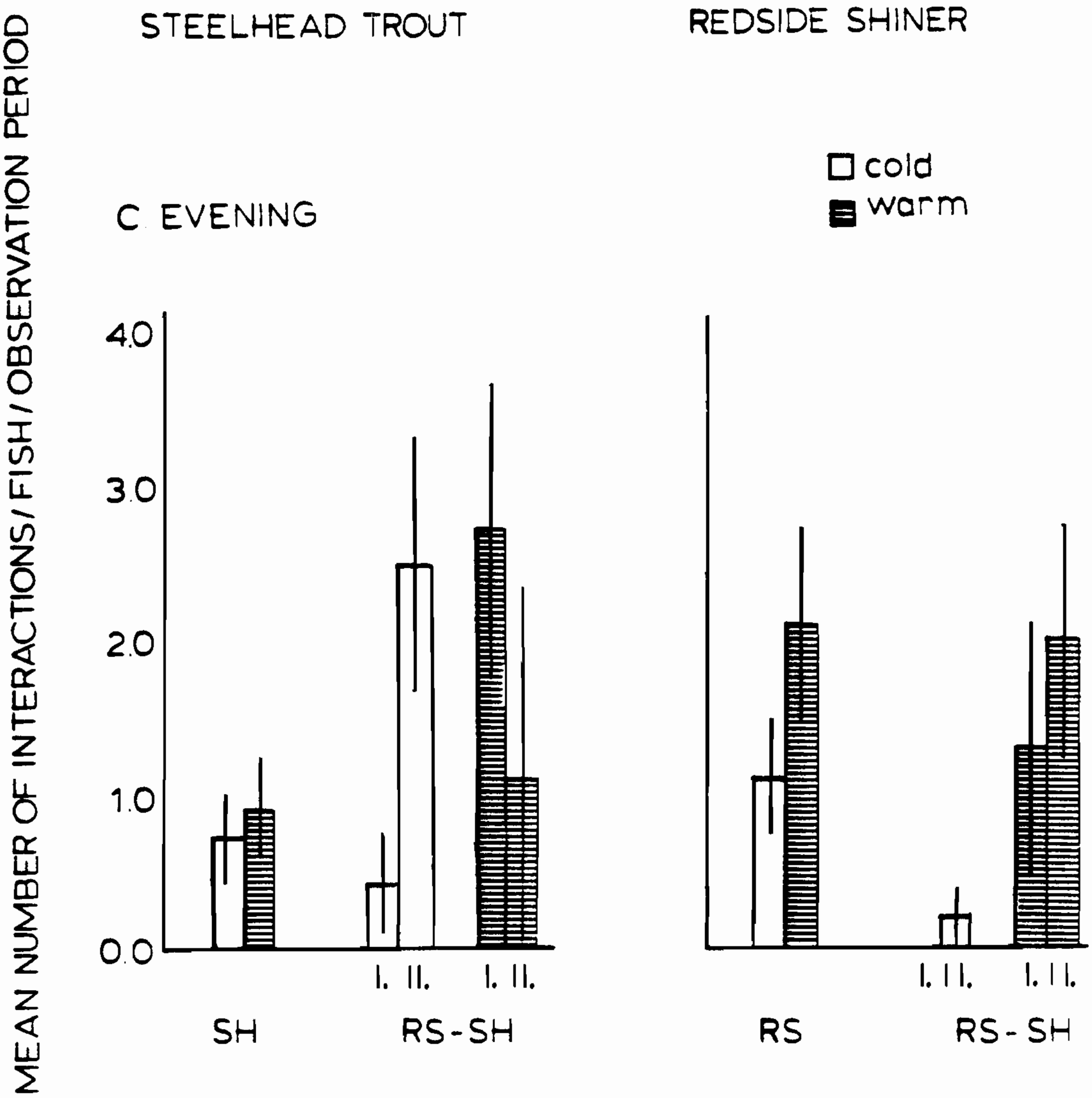

Fig. 5. (continued)

in RS-SH.I or when alone. Mean numbers of interactions per fish per observation period in RS-SH.I and in the SH trial were not different (ANOVA $P>0.05$) at any time of day. Number of interactions per trout in the morning and evening were different (ANOVA $P<0.05$), however, between RS-SH.II and the SH trial. These diffferences resulted because of the large number of interspecific interactions initiated by the trout and not an increase in the number of intraspecific interactions. There was no difference (ANOVA $P>0.05$) between the number of intraspecific interactions initiated when shiners were present and the number of interactions initiated when trout were alone. There were, however, more interspecific interactions (ANOVA $P<0.05$) at both times in RS-SH.II than interactions at corresponding times when trout were alone. In both trials at cold temperatures, trout aggressively responded to any shiner that attempted to enter their territory, especially during feeding periods. Trout chased or nipped intruding shiners, which usually fled to the nearest pool.

Activity levels of redside shiners decreased in the presence of steelhead trout at cool water temperatures. There were fewer interactions initiated by shiners in both RS-SH trials (ANOVA $P<0.05$) than in the cool trial when they were alone (Fig. 5). The social organization of the shiners also changed in the presence of trout (Reeves et al. in prep.) Many shiners were territorial and interacted with any fish that attempted to enter or move through their territory when trout were absent. In the presence of trout, shiners did not defend territories but formed a loosely structured group, primarily in the most downstream pool of the channel and were much less aggressive toward other shiners. Only 4% (6/145) of the total interactions initiated by shiners were directed towards trout and all but one were observed in the evening.

At cool water temperatures, there was a noticeable increase in activity of redside shiners in the latter stage of evening, when daily water temperatures were highest. Groups of 4 to 7 shiners began moving from the last riffle and pool to all areas of the channel. Steelhead trout at the same time began to move off riffles into pools or cover on a riffle, as occurred when trout were observed alone. Trout made very few attempts to interfere with shiners at this time. Shiners were observed picking at the substrate, both on riffles and in pools. This type of behavior was observed even during complete darkness by use of a dim red light. Shiners were again found primarily on the back of the last riffle and in the last pool by first light. This pattern was not observed when shiners were alone at cool temperatures or at any time at warm temperatures when trout were present or absent.

Number of interactions initiated by redside shiners at warm water temperatures, in general, was not influenced by the presence of steelhead trout. There were no differences in the number of interactions per shiner per observation period (ANOVA P>0.05) when shiners were alone and when trout were present, except in the morning in RS-SH.I (Fig. 5). There were fewer interactions per fish

(ANOVA $P<0.05$) in the presence of trout. Only 1% (17/1437) of the total interactions initiated by shiners in the two RS-SH trials were directed towards trout. These were predominately nips and chases (Reeves et al. in prep.).

The effect of steelhead trout on movements of redside shiners varied with water temperature. At cool temperatures, movement of shiners was less (ANOVA $P<0.05$) at all times of the day when trout were present compared to when trout were absent (Fig. 6). At warm temperatures, however, movement of shiners with trout present did not differ from when trout were absent (ANOVA $P>0.05$) (Fig. 6). Movement of shiners, when alone, was not affected by water temperatures during feeding periods but did differ during the non-feeding period (Fig. 6). Numbers of shiners moving across riffles at each temperature were not different (ANOVA $P>0.05$) in the morning and the evening but there was more movement (ANOVA $P<0.05$) in the cool channel at midday than in the warm one.

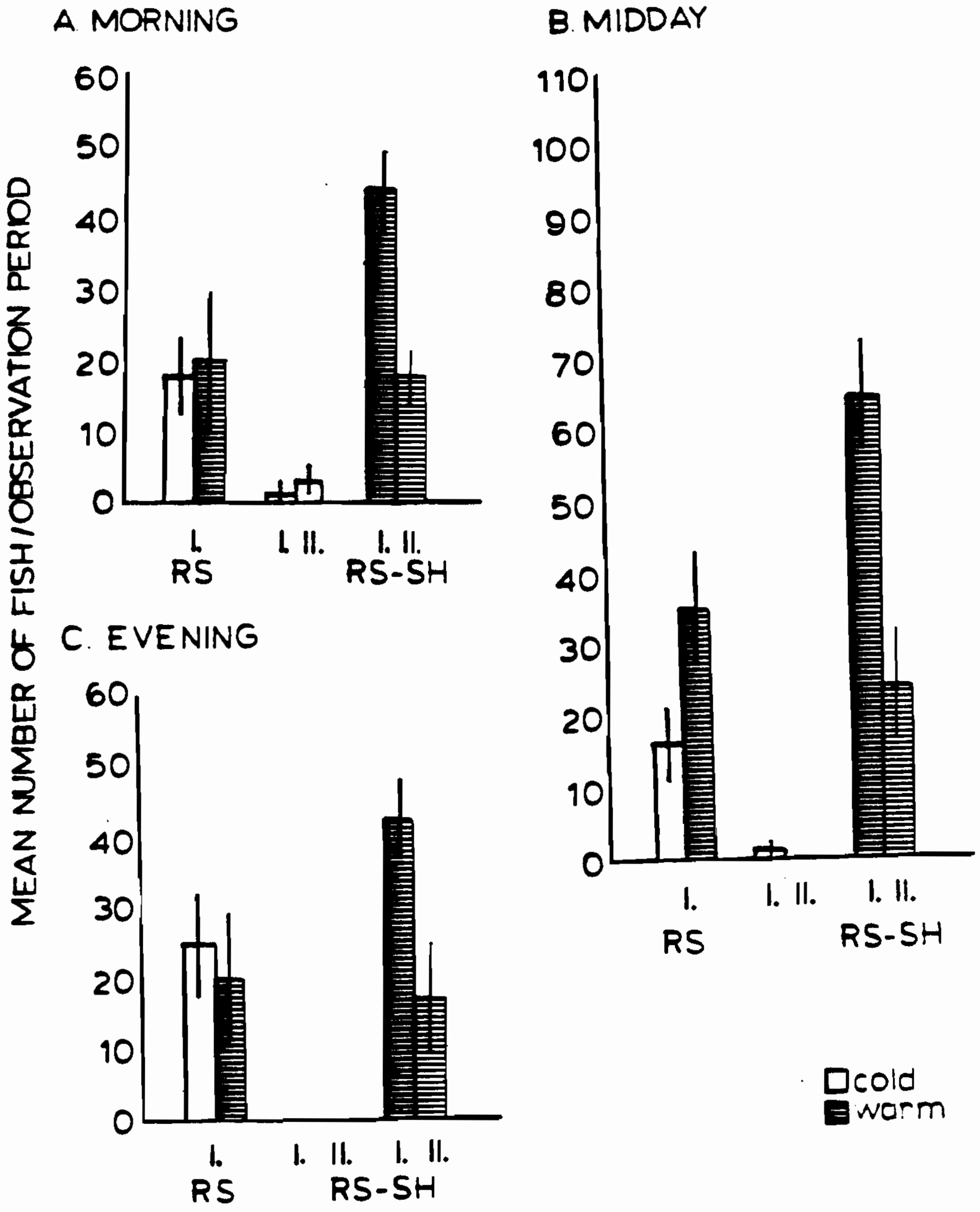

Fig. 6. Mean number of redside shiners moving across riffles per observation period (5 min) at each time of day when steelhead trout were present or absent at different water temperatures in laboratory streams. Vertical bars represent ±2 SE.

Distribution

Distribution of steelhead trout within the channel differed with water temperature when they were alone. Trout were evenly distributed between the upstream and downstream halves (i.e. an equal number of fish in the upstream half and in the downstream half) at cool temperatures (Fig. 7A). A single trout occupied each of the last three riffles and the front of the most upstream pool during feeding periods. When food was absent, fish moved to cover on the riffle where they had been observed feeding or to the head of the pool immediately downstream from the riffle. Distribution was different ($P<0.01$) in the warm channel, however. Trout were primarily restricted to the two downstream riffles; seldom were trout observed in the upstream half of the channel (Fig. 7D). Despite this crowding at warm temperatures, there were no differences between the total numbers of behavioral interactions per individual per observation period at the two temperature regimes (Fig. 5).

Distribution of redside shiners in the laboratory streams, when alone, differed with water temperature and time of day. Shiners were evenly distributed ($P>0.05$) in the upstream and downstream halves of the channel during feeding periods at warm temperatures (Fig. 7E). At midday, however, when there was little food circulating, there were more shiners ($P<0.05$) in the back half of the channel. Distribution was more varied at cool temperatures. Fish were evenly distributed in the morning ($P>0.05$) (Fig. 7B), but

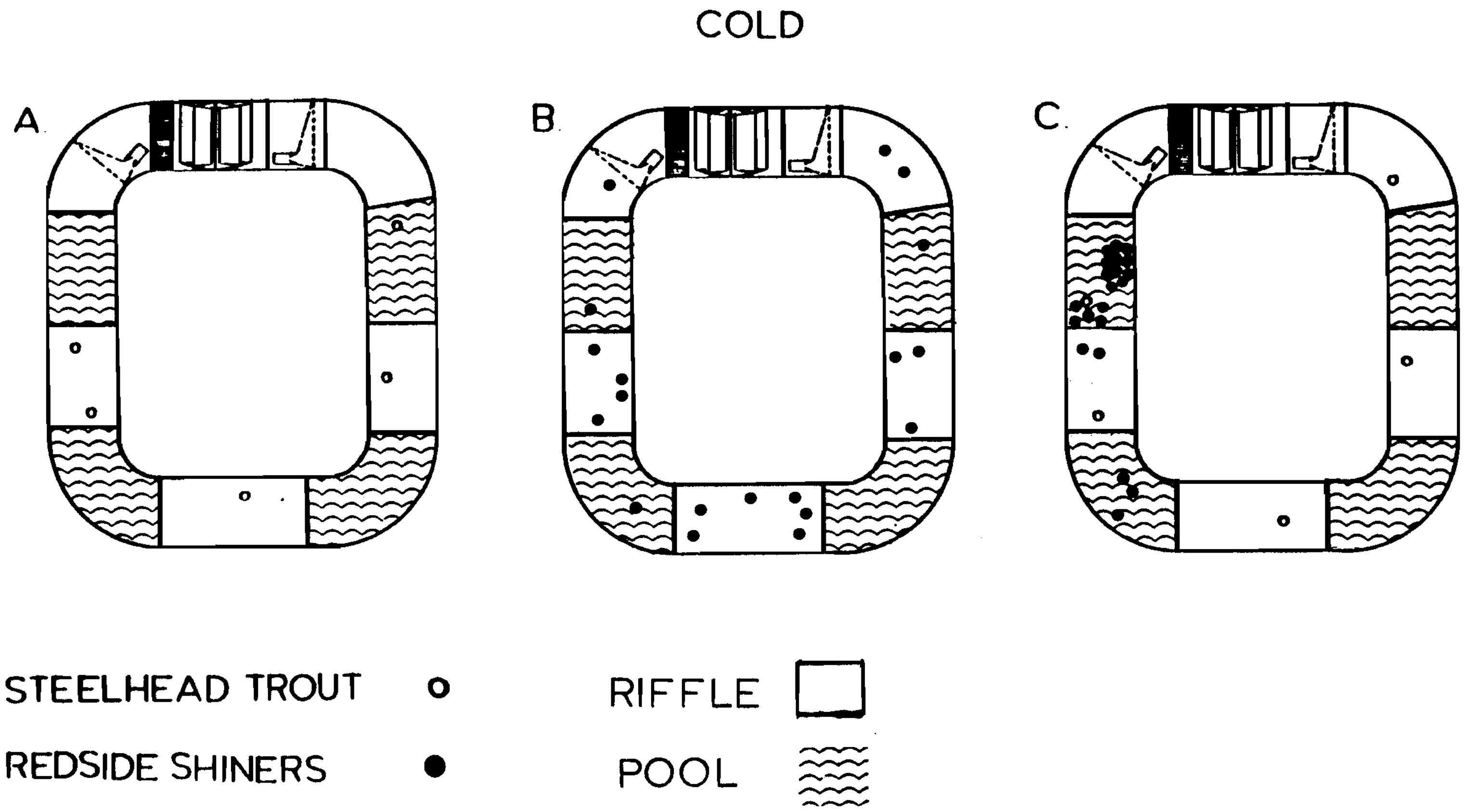

Fig. 7. Distribution of redside shiners and juvenile steelhead trout in laboratory streams during feeding periods.

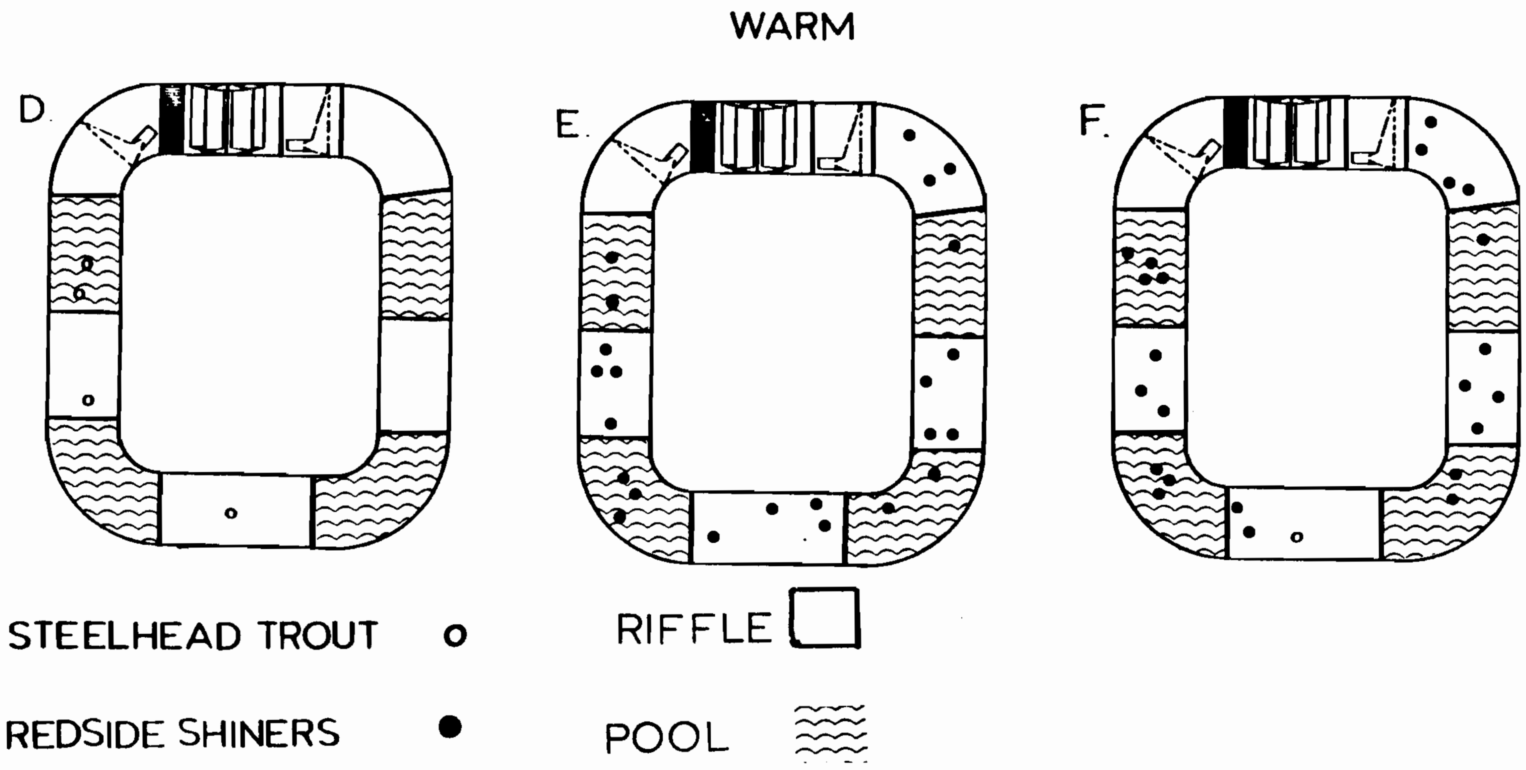

Fig. 7. (continued)

there were more fish ($P<0.05$) in the downstream half of the channel at midday, similar to the warm channel, and in the upstream half ($P<0.05$) in the evening. Shiners were observed primarily on riffles during feeding periods in both temperature regimes. Fish generally moved into pools or swam about the channel in groups of 3-4 similar sized individuals when food was not present.

At cool water temperatures, distribution of steelhead trout was not affected by redside shiners but the distribution of shiners was restricted when trout were present (Fig. 7C). Trout in both RS-SH trials were evenly distributed ($P>0.05$) around the channels at all times and inhabited the same habitats as in the SH trial. Shiners remained in the back half of the channel ($P<0.01$), primarily on the back of the last riffle and in the last pool during daylight.

Each steelhead trout that remained in the channel at warm water temperatures when redside shiners were present occupied a riffle but in different parts of the channel. The smaller fish, in RS-SH.II, was restricted to unfavorable turbulent habitat on the most upstream riffle. This fish attempted to move to riffles further downstream but was always harrassed and driven off by shiners. The fish in RS-SH.I successfully maintained a territory on riffle 3 (Fig. 7F), which was a more favorable area than the most upstream riffle, but also initiated more interactions than the other trout (Fig. 5).

At warm water temperatures, there were differences in distribution of redside shiners at certain times of the day when steelhead trout were present. Distribution in RS-SH.I (Fig. 7F) was similar to the warm RS trial, i.e. no difference ($P>0.05$) in the morning and evening but more shiners in the back half of the stream ($P>0.05$) at midday. There were no differences in distribution ($P>0.05$) in RS-SH.II in the morning and midday but there were more shiners in the back half of the channel in the evening ($P<0.05$). Shiners continued to inhabit both pools and riffles in the same manner described previously in the RS trial.

DISCUSSION

Effects of water temperature on the production and behavior of redside shiners and juvenile steelhead trout differed. Production by trout in laboratory streams was greater at cold temperatures than at warm temperatures. This is consistent with the result of other studies that examined the impact of elevated water temperatures on growth of juvenile anadromous salmonids in laboratory streams (Averett 1969; Bisson and Davis 1976; Hughes 1979). Distribution of trout in laboratory streams was more restricted at warm temperatures than at cool temperatures. Production by redside shiners was greater at warm temperatures than at cool temperatures. There was no difference in distribution of shiners in laboratory streams at warm and cool temperatures, but shiners were more active at warm temperatures. In natural streams, each species occupied similar habitats in allopatry, where the primary difference among streams was water temperature. Cool water temperatures favored trout and warm temperatures favored shiners.

The outcome of competitive interactions between redside shiners and steelhead trout was influenced by water temperature. Trout were the dominant fish at cooler temperatures. In the field, trout occupied similar, but statistically different, habitats when alone at cool temperatures and when shiners were present at intermediate temperatures. Neither habitat distribution or production by trout in laboratory streams was affected by the presence of shiners at cool temperatures. Shiners in the presence of trout at cool temperatures used different habitats from those used when trout were absent. Shiners adapted to the restricted distribution by adjusting their social behavior so that there was less intraspecific aggression and by increasing activity at night. Also, shiners appeared to feed on benthic organisms in the field. Production by shiners at cool temperatures in the laboratory streams probably would have been greater when trout were present if more food types, such as benthic organisms, had been available. In the field, shiners moved into faster waters at midday, where they appeared to be actively feeding. Trout were less active at midday than in the morning or evening, when invertebrate drift is greatest (Waters 1969), and made no attempt to prevent shiners from feeding. Hixon (1980) found that two reef fish, *Embiotoca jacksoni* and *E. lateralis*, co-existed because *E. jacksoni* avoided *E. lateralis* in areas where their ranges overlap. *E.* lateralis occupied areas of preferred food but *E. jacksoni* foraged in these areas when *E. lateralis* was temporally absent. Hixon speculated that the benefits to *E. jacksoni* of avoiding *E. lateralis* were greater than the benefits of utilizing other areas. In the present study, it appears that the advantages to shiners of avoiding trout were greater than any gains that might have been realized from moving to other areas of the stream.

The redside shiner was the dominant species at warm water temperatures. Production by shiners was greater and decreased less, on a relative scale, in the presence of steelhead trout at warm temperatures than at cool temperatures. Shiners occupied similar habitats in laboratory streams when trout were present or absent at warm temperatures and there were no differences in activity levels. These habitats were the same habitats occupied by trout at cool temperatures. In the field, shiners in allopatry inhabited areas similar to those occupied by trout in allopatry. Shiners, when alone, were not active at night at warm temperatures in either the field or laboratory. Juvenile salmonids were present early in the year in the stream where we observed shiners alone. We did not observe any direct confrontations between shiners and salmonids but it is possible that shiners displaced the salmonids as the season progressed and water temperature increased. Unlike shiners, which remained in the system in the presence of trout at less favorable temperatures, trout did not make behavioral adjustments that would have allowed them to remain but instead migrated from the laboratory channels and probably from the field sites also.

The steelhead trout that remained in the laboratory streams in the presence of redside shiners at warm water temperatures were not the largest trout introduced. Larger individuals migrated soon after shiners were introduced. Larger individuals generally dominate social systems of juvenile salmonids (Chapman 1962; Mason and Chapman 1965). Larger trout may have migrated because they were more susceptible to F. columnaris than were fish that remained and/or had difficulty obtaining sufficient amounts of food. At warm temperatures, shiners responded more quickly to food items than did trout. The trout that remained were smaller than most migrants and therefore did not require as much food for maintenance and growth. Growth of the trout that remained in the channel indicates that they were able to obtain adequate amounts of food and they were not susceptible to F. columnaris.

The primary element of competition responsible for the dominance of each species differed. Steelhead trout prevailed at cool water temperatures by interference competition, which refers to any activity that restricts the access of a competitor to a contested resource (Miller 1967). Trout were strongly territorial and prevented or severely limited access of redside shiners to food. Total production by shiners decreased as a result of this restricted distribution. The energetic cost to trout of interacting with shiners at cool temperatures appeared to be minimal. Total production by trout was the same whether or not shiners were present, even though trout initiated significantly more interactions in the presence of shiners than they did in their absence. Shiners in the field at intermediate temperatures and in laboratory streams at cool temperatures occupied different habitats in the presence of trout than they did when trout were absent. These habitats were slower deeper areas, where food was less abundant than in riffles or glides, which shiners inhabited in the abscence of trout. Shiners also adjusted to this restricted distribution by changing their social behavior and by being active at night.

Shiners dominated at warm temperatures by exploitation competition, which is the ability to better or more efficiently exploit a resource (Miller 1967) and to a limited extent by interference competition. Shiners were more active at warm temperatures and responded more quickly to food items than did trout. Only one trout resided in the laboratory stream when shiners were present at warm temperatures while four remained when shiners were absent at warm temperatures and 5-6 when trout were present at cool temperatures. At warm temperatures when shiners were present, trout would initially attempt to maintain a territory. The activity level of shiners was higher and many shiners were able to occupy positions on riffles. As a result, most trout abandoned their attempt to maintain a territory within 2-3 days in an attempt to feed and they began to move about the channel. Only one trout remained by day 4 when shiners were present at warm temperatures and total production by trout decreased in the presence of shiners compared to when when shiners were absent. Total production by shiners at warm temperatures was the same when trout were present or absent and was greater than any condition at cool temperatures. Crossman (1959) reported shiners to be more active feeders than rainbow trout in laboratory troughs. Baltz et al. (1982) found that speckled dace were better able to adjust metabolically to higher temperatures than were riffle sculpins, which were stressed at warm temperatures but dominated interspecific encounters with dace at cooler temperatures. We did not attempt to determine the reason for such variation in shiner activity at the different temperatures but we surmise that the scope for activity (Fry 1947) of shiners was greater at warm temperatures than at cold temperatures. Salmonids, on the other hand, are stressed at warmer temperatures (Brett 1952) and were unable to interact successfully with shiners.

Change in habitat utilization between sympatry and allopatry does not necessarily imply interactive segregation (Nilsson 1967) or competition between two species. Shifts in habitat utilization may be due to differences in physical environments between areas as well as biological interactions (Sale 1979; Connell 1980). Physical characteristics of the three field study areas were not statistically different ($P>0.05$) but this does not imply that the shift in habitats utilized by redside shiners in sympatry was due entirely to interference competition by steelhead trout. Study areas were not exactly the same in physical composition. Deeper areas were more prevalent in the stream where the species occurred together than at the other sites. Trout in sympatry occupied areas that were slightly deeper than areas occupied in allopatry. The presence of predators when the species were observed in sympatry may have also caused the fish to move to deeper areas. It would appear, therefore, that some of the habitat shift by shiners may be attributable to physical differences among sites and/or the presence of predators, but the primary reason for the habitat shift by shiners was probably interference competition by trout.

Hurlbert (1984) criticized many ecological studies that involved field experiments because of their lack of replication of treatments, among other things. He questions the validity of results from studies that lack replication and their application to other areas or systems. In our study, data were collected from only one site on each of three streams that differed primarily in their past land-management practices and water temperature regimes. We spent two years prior to this study observing steelhead trout and redside shiners at other sites along the study streams and in a number of other streams throughout western Oregon. Distributions, activity patterns, and behaviors of both species in these other streams were similar to those observed in the study streams and laboratory channels. We believe, therefore, that results from this study are applicable, at least in general terms, to other stream systems in western Oregon and other parts of the Pacific Northwest, even though we collected detailed data from only one stream at each temperature regime.

Interactive segregation generally occurs in the early stages of contact between ecologically similar species (Nilsson 1967). Over time, the species may evolve towards selective segregation or the elimination of one of the species. It appears that redside shiners and steelhead trout have existed in streams throughout the Columbia River basin of Oregon for at least the last 10,000 years (Dr. C. E. Bond, Dept. of Fisheries and Wildlife, Oregon State Univ., Corvallis, OR. 97331, pers. comm.). Smith (1975) found fossils of ancestral shiners and salmonids together in early Pliocene formations in southwest Idaho. It is not clear how long the two species have coexisted in the Umpqua River system. We believe contact between the two species was probably minimized historically because of environmental conditions (i.e areas of warm water were minimal). Frequency and intensity of contact between the two species, and between other anadromous and resident salmonids and shiners, have probably increased substantially during the last 50 to 75 years as a result of changes in environmental conditions attributable to human activity, such as increased water temperature.

Increased susceptibility to disease, as influenced by water temperature, may have modified interactions between redside shiners and steelhead trout; one species in the presence of the other at unfavorable temperatures was more susceptible to _F_. _columnaris_. Most migrant trout were infected with _F_. _columnaris_ at warm temperature while more than half of the migrant shiners were infected at cool temperatures. We can only speculate on the reason why this occurred. Additional stress caused by the presence of a competitor in a less favorable environment may cause an organism to be more prone to disease. Holt et al. (1975) found that susceptibility of juvenile anadromous salmonids to _F_. _columnaris_ increased with increasing water temperature. Influence of water temperature on the susceptibility of shiners to _F_. _columnaris_ is not known at present. Non-game fish, including redside shiners, in a cool tributary of the McKenzie River, OR. suffered high mortality rates from F. columnaris while resident salmonids were not affected (Dr. A. Amandi, Dept. of Microbiology, Oregon State Univ., Corvallis, OR. 97331, pers. comm.). Park (1948) found that the outcome of competition between two species of beetles was influenced by the presence of a sporozoan parasite. Disease or susceptibility to disease may be an important factor influencing the outcome of interspecific encounters between fish, and other organisms. In this study, the extent of influence of F. columnaris on the outcome of competitive interactions between trout and shiners is not known exactly but it appears to have been fairly strong.

The water temperature regime of large, mid-order streams may be altered by cumulative changes in water temperature in headwater and lower order streams that result from land-management activities. Many studies have examined the on-site effect of land-management activities in small, lower order streams (Hall and Lantz 1969; Burns 1972; Holtby and Newcombe 1982; Hawkins et al. 1983). Although salmonid populations may respond favorably to opening of the riparian canopy (Hawkins et al. 1983) and/or increased water temperatures (Burns 1972) resulting from management activities in these streams, the cumulative effect of these changes on other areas of the watershed has received little or no consideration. Water temperature in mid-order streams lower in a watershed is dependent to a large degree on the temperature of water entering from upstream. Mid-order streams are important rearing areas for juvenile anadromous salmonids, especially chinook salmon and

$\geq 1^{+}$ steelhead trout. They also have a more diverse fish community than do lower order streams (Vannote et al. 1980). Changes in environmental conditions may result in a decrease in available habitat for salmonids, and/or alter the outcome of interactions between salmonids and potential competitors. Environmental changes less favorable to salmonids, such as increased water temperature in higher order streams, could offset any increase in abundance or production of anadromous salmonids that might occur from opening the canopy along lower order streams, or could even result in an overall decrease in the population.

Results from this study support the contentions of Baltz et al. (1982) that we need to consider the biological implications to fish communities of altering environmental conditions. We need to evaluate the usefulness of models that consider each species separately and that assume that the species responds solely to changes in the physical environment (e.g. Bovee and Milhous 1978). More realistic models that consider the impact of environmental alterations on the fish community as a whole need to be developed. We also need to evaluate the usefulness of programs designed to control undesirable species by chemical or mechanical means. The best program for the management of both desired and undesired species is one that creates and maintains optimum conditions for the favored species. This will require the implementation of sound land-management policies throughout a watershed.

Social Behavior of the Redside Shiner (*Richardsonius balteatus*) in Western Oregon

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ABSTRACT

The redside shiner exhibited two basic social organizations, loose aggregations and defense of an area. The type of organization observed varied with water temperature, abundance of food, and presence or absence of juvenile steelhead trout. The behavioral repertoire of the redside shiner was diverse. Size of the individual and proprietorship of an area were important in determining outcomes of interactions. Intensity of individual encounters varied with conditions in the laboratory streams. Plasticity of its social behavior appears to contribute to the ecological success of the redside shiner.

INTRODUCTION

Study of the behavior of an organism provides insight into the organism's adaptation to its environment. The redside shiner (*Richardsonius balteatus*), a cyprinid, is widely distributed in lakes and streams in the Pacific Northwest (Scott and Crossman 1973). It has received much attention because of its ability to successfully compete with rainbow trout (*Salmo gairdneri*) in lakes (Larkin and Smith 1954; Crossman 1959; Johannes and Larkin 1961) and because of its morphological variability (Scott and Crossman 1973). The social behavior of this ecologically successful species has not been studied, however.

The purpose of this paper is to describe the social behavior of the redside shiner, which is diverse and complex. Observations on shiner behavior were made concurrently with a study that examined the influence of water temperature on interactions between shiners and juvenile steelhead trout (*Salmo gairdneri*) (Reeves et al. in prep.). Many of the agonistic displays of shiners described in this paper are similar to those exhibited by juvenile salmonids. As a result, much of the terminology used is taken from literature describing social behavior of juvenile salmonids, particularly Hartman (1965). The descriptions characterize the major behavioral displays but each component could undoubtedly be classified on a more refined scale in a study designed specifically for that purpose.

METHODS AND MATERIALS

All work was performed in two laboratory streams located at the Forestry Sciences Laboratory, USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Corvallis, OR. and described by Reeves et al. (1983; in prep.). Redside shiners were observed at two different diel water temperature regimes, 12-15^{o}C (54-59^{o}F) and 19-22^{o}C (67-72^{o}F). Two trials with steelhead trout present and one with trout absent were run at each temperature regime. Size of shiners varied slightly in each trial, ranging from a mean (±1 SD) of 71.5 mm (± 12.0) (fork length) and 4.8 g (±2.2) to 77.2 mm (±9.9) and 5.5 g (±2.1). Number of fish observed in a given trial ranged from 24 to 33. Fish were captured by seining and electoshocking and were held 2-3 weeks before introduction to the channels. Test periods were 13 days. A photoperiod of 15 hours light and 9 hours of complete darkness was used. The light phase consisted of 1.5-hour "morning", where lights gradually increased from zero to full intensity, 12 hours of full intensity, and a 1.5-hour "evening", where lights gradually dimmed to zero intensity. Observations were made three times daily, during the morning and evening feeding and just before the midday feeding. Frozen brine shrimp was the sole food source and was delivered via a PVC pipe that ran along the bottom of the channel. Procedures and materials are described in further detail by Reeves et al. (in prep.).

During a 35-minute period, fish in each pool and each riffle in a channel, except for the most upstream riffle, were observed for 5 minutes. The order in which the observations were made was randomly determined at the start of each session. The lower channel was always observed first. Light cycles were staggered by 45 minutes so that each channel could be observed under similar light conditions. The number and location of individual fish in each area were noted and the number and type of behavioral interactions, both intra- and interspecific, were recorded. When shiners were observed alone, we recorded size of individuals involved in an interaction and classified them into two categories, similar sized individuals, which involved fish with less than 1 cm difference in length, and different sized individuals. Only intraspecific interactions are described in this paper because the number of interspecific interactions (i.e. those initiated by shiners and directed toward steelhead trout) was only 1.4% (23/1585) of the total number of interactions observed when trout were present. Interspecific interactions involved the same types of behaviors as intraspecific interactions.

RESULTS

Redside shiners exhibited two types of social organization, which varied with the presence or absence of steelhead trout and with water temperature. At cool temperatures in the presence of trout, shiners formed loose aggregations on the back of a riffle or at the head of a pool in the most downstream section of the laboratory stream. There were the fewest interactions between individuals in this trial. Those that were observed were much less intense than those that occurred at warmer temperatures or when trout were absent at cool temperatures. At cool temperatures in the absence of trout and at warm temperatures, some shiners defended areas on riffles, driving fish away that attempted to move into or through the general area. Shiners that defended an area were generally larger individuals. In some instances dominant individuals had a darker, more distinct band along the lateral line than did subordinates. Dominants also appeared to have a more silvery appearance than subordinates. It appeared that some individuals defended the same general area for extended periods but we did not mark individual shiners and were unable to accurately identify individuals. We were unable to discern the boundaries of an area defended by an individual shiner but it appeared that the boundaries were much more flexible than those of trout territories. Shiners that did not hold an area either moved about the channel in search of food or formed loose aggregations on the back of riffles or at the head of pools as described previously.

Individual components of the social behavior of the redside shiner varied in complexity and frequency of occurrence. The following are descriptions of the different behaviors observed:

Parallel display involved two individuals, one attempting to hold or maintain a preferred position on a riffle or in a pool and the second either attempting to establish a territory in the same area or traverse through the occupied territory. The display began with fish swimming parallel to each other in a straight line (Fig. 8A). Individuals were close together, generally within 2 cm. The fish swam quickly, generally upstream and with exaggerated body movements. Fins were erect, similar to the dominant salmonid in a lateral display (Fabricius 1953; Kalleberg 1958), and the lateral line was straight. After a short distance, they crossed over top of and under each other, resembling a braided pattern (Fig. 8B). Distance traveled by individuals involved in a parallel display varied from 0.1 to 1 m. Eventually one individual depressed its fins and moved away (Fig. 8C) and the dominant individual returned to the area where the encounter began.

Parallel displays generally occurred when a fish moved into the area of an adjacent fish. Parallel displays were almost exclusively between similar sized fish (91.3%). In encounters between similar sized individuals, it appeared that the proprietor of the contested area dominated. Larger fish prevailed in parallel displays between different size individuals, even if the smaller individual had been in the area before the larger one.

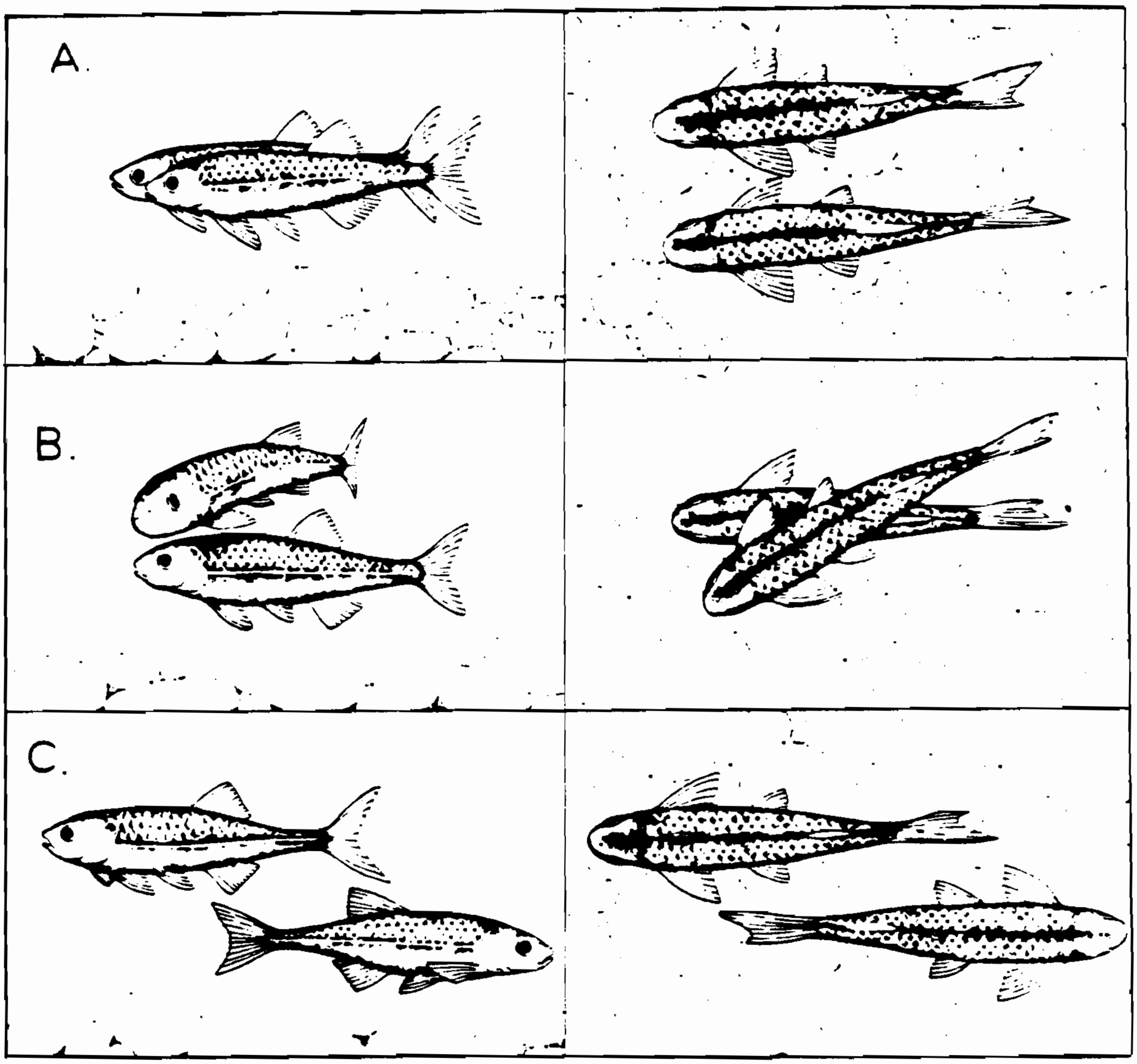

Fig. 8. Parallel display of the redside shiner. (A) Behavior began with fish swimming parallel to each other with fins held erect. (B). Fish crossed over top of and under each other. (C). Loser depressed fins and left contested area. See text for more detail.

Eviction involved the physical displacement of one fish by another. The two fish began moving upstream, parallel to each other, their movements resembling the beginning of a parallel display (Fig. 9A). Fins of both fish were held erect. After a short distance, generally less than 25 cm, the dominant fish moved one-half to one body length in front of the other fish (Fig. 9B). The dominant fish then turned 45 to 90° to the subordinate's snout so that the side of the dominant touched or nearly touched the subordinate's snout (Fig. 9C). The dominant forced the subordinate downstream and away from the contested area.

Evictions occurred, as did parallel displays, when one fish moved into the area of an adjacent fish. Evictions were observed with about equal frequency between similar sized (49.0%) and different sized individuals (51.0%). It was difficult to identify a feature of the dominant in encounters between similar sized individuals. When size of the fish differed, larger individuals generally prevailed, but in a few instances smaller fish prevailed if they were in the area first.

Chase involved the aggressive pursuit of one fish by another. Fins of the aggressor were erect. Chases varied from low intensity ones that covered short distances, 0.1-0.2 m, to very intense encounters that covered 1.0-1.5 m. The dominant fish in interactions between similar sized individuals was generally the individual holding the area where an encounter began. Chases occurred about equally between the two size categories, 48.5%

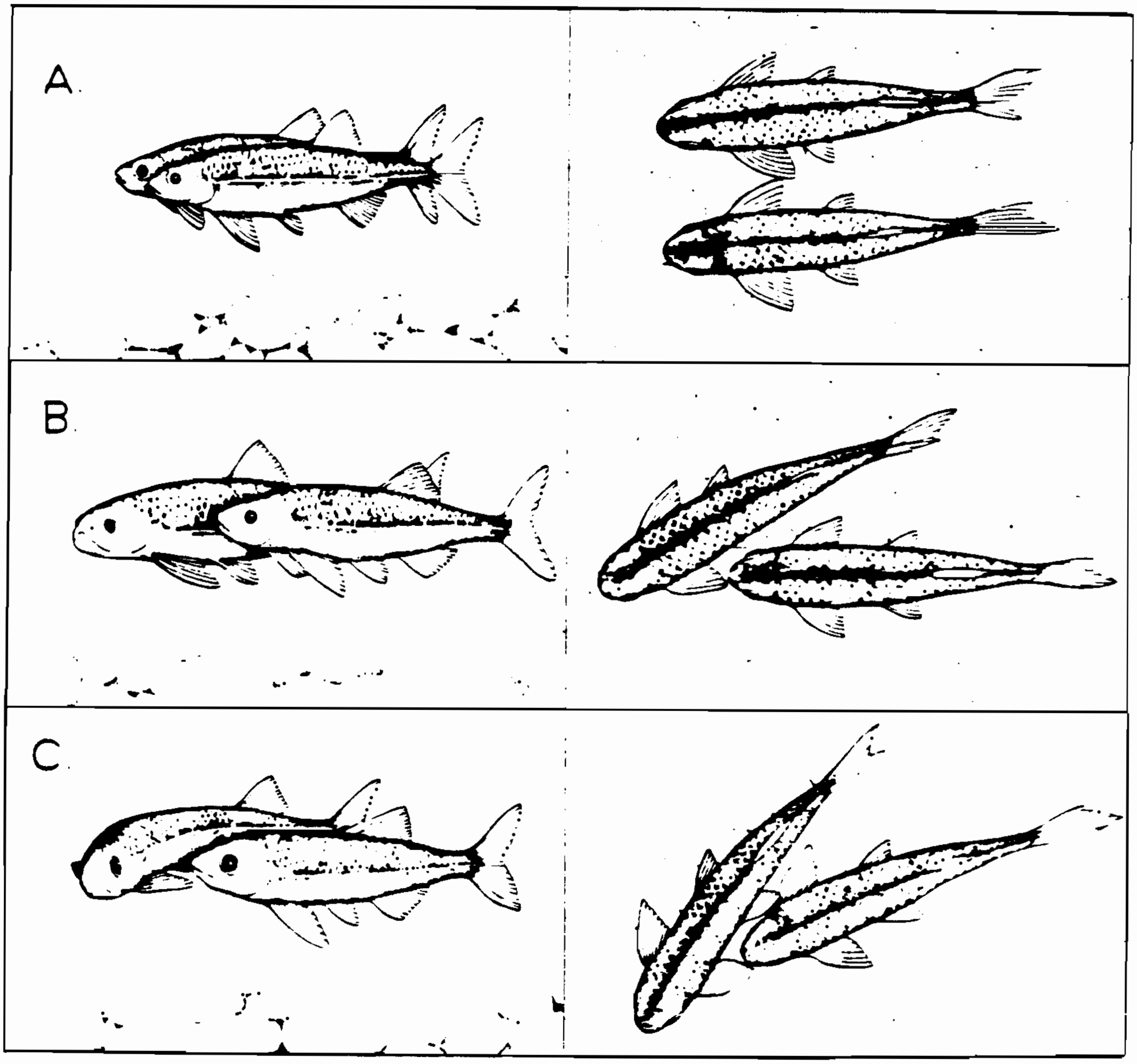

Fig. 9. Eviction behavior of the redside shiner. (A). Behavior began with fish swimming parallel to each other with fins erect. (B) Dominant moved one-half to one body length ahead of subordinate and (C) turned 45-90° so that side touched or nearly touched snout of subordinate. Subordinate forced downstream, away from contested area. See text for more detail.

between similar sized fish and 51.5% between different sized individuals. Larger fish prevailed in interactions between different sized individuals. Chases often ended with the aggressor nipping the other fish.

Nip was a behavior, generally of high intensity, in which the aggressor made definite mouth to body contact with the other fish. This was the same definition given by Hartman (1965) for juvenile steelhead trout and coho salmon (Oncorhynchus kisutch). Nips occurred when one fish attempted to move into or through a defended area. Often the intruder was nipped several times before it would abandon attempts to move into an area. Nips by redside shiners were directed primarily towards the head region of the receiving individual. This differed from nips by steelhead trout, both in inter- and intraspecific interactions, which were directed primarily at the body. Nips occurred most frequently between fish of different sizes (62.0%). Larger fish almost always nipped smaller fish; the reverse was seldom observed. We never observed a behavior similar to the threat nip that Hartman (1965) described for steelhead trout and coho salmon.

Intention moves (Hartman 1965) occurred when one fish made a short lunge at another but there was never any contact between individuals. The aggressor had its mouth open and gill covers flared. The fish to which the movement was directed moved away. Intention moves were observed to occur about equally between similar sized (52.4%) and different sized individuals (47.6%). The proprietor of a contested area generally prevailed when fish were the same size. Intention moves between fish of different sizes were almost always larger fish threatening smaller individuals.

Threat behavior occurred when one individual turned toward another individual with its mouth open and gill covers flared, as in an intention move, but made no directed movement toward the the other fish. The threatened fish generally moved away. Most threats (61.6%) were between dissimilar sized individuals and were generally initiated by the larger individual. As in most of the other behaviors, proprietors generally prevailed.

The number of interactions by redside shiners varied with water temperature, presence or absence of steelhead trout, and presence or absence of food (Table 5). The greatest number of interactions occurred during feeding periods at warm temperatures. Activity levels decreased when food was absent in all situations. The fewest interactions between shiners were observed at cool temperatures in the presence of trout.

Types of behaviors varied with the presence or absence of food. At both water temperature regimes and in the presence or absence of steelhead trout, nips were the dominant behavior during feeding periods (Fig. 10). Nips comprised 66% or more of the total interactions except in the evening at cold temperatures when trout were present. Evictions were the most common behavior at this time. During non-feeding periods (i.e. midday), evictions were the dominant behavior type (Fig. 10B,E) except when shiners were alone

Table 5. Number of intraspecific interactions per redside shiner[a] per observation period (5 min) in laboratory streams. Total number of interactions observed during test period shown in parenthesis. I and II refer to the first and second trial, respectively, run at each temperature regime.

Time		Morning	Midday	Evening
shiners alone				
warm temperatures		2.5 (588)	0.86 (138)	2.1 (471)
cool temperatures		1.1 (348)	0.14 (25)	1.1 (306)
shiners with steelhead trout present				
warm temperatures				
	I.	1.2 (187)	0.32 (40)	1.3 (196)
	II.	2.5 (468)	0.77 (135)	2.0 (411)
cool temperatures				
	I.	0.09 (16)	0.01 (1)	0.03 (7)
	II.	0.23 (40)	0.04 (8)	0.23 (53)

[a] Does not include redside shiners that were observed under cover during the observation period.

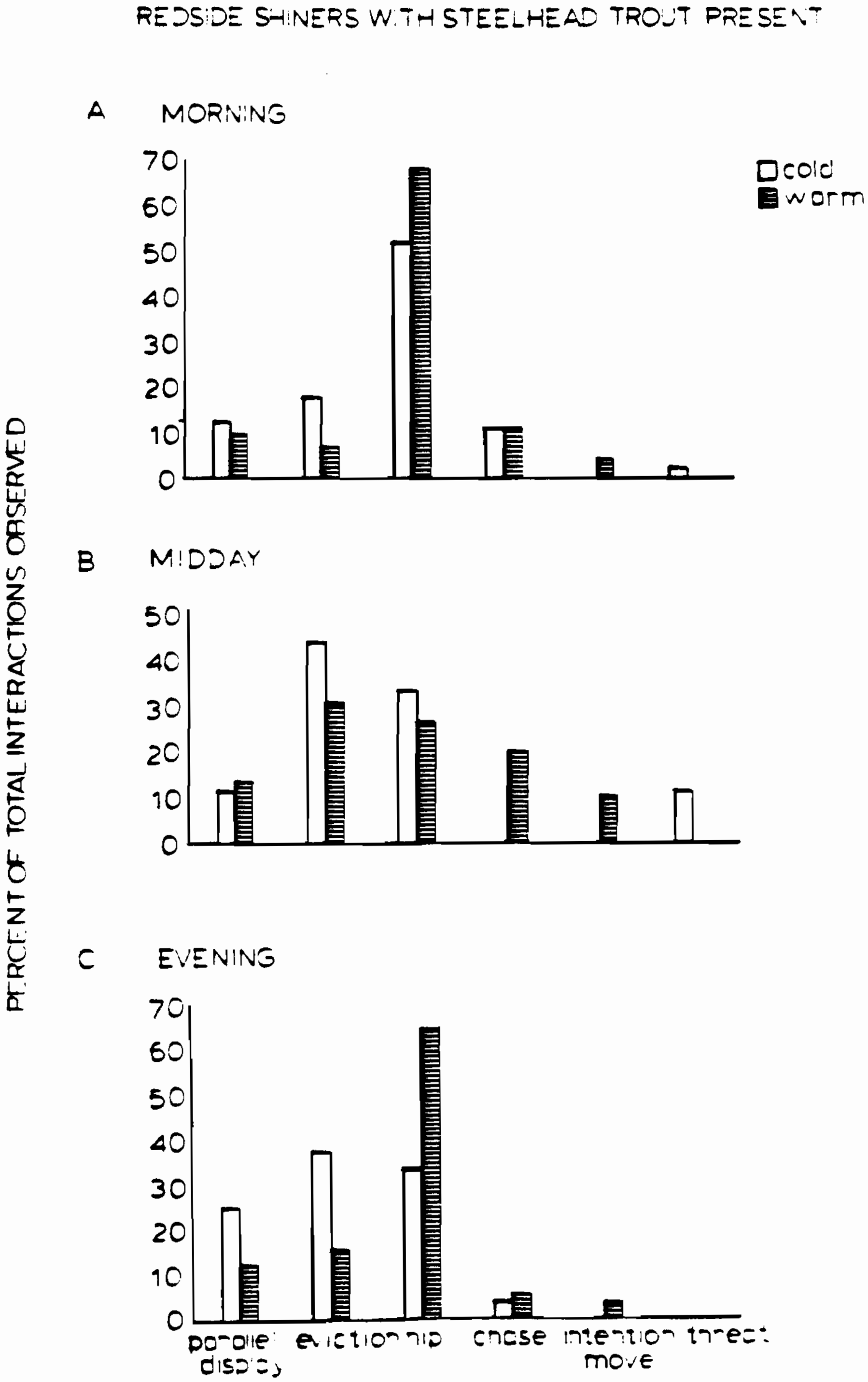

Fig. 10. Percent of each behavior type observed at each time of day at different water temperatures when steelhead trout were present or absent in laboratory streams. Total number of intraspecific interactions observed at each time of day during test period are shown in Table 5.

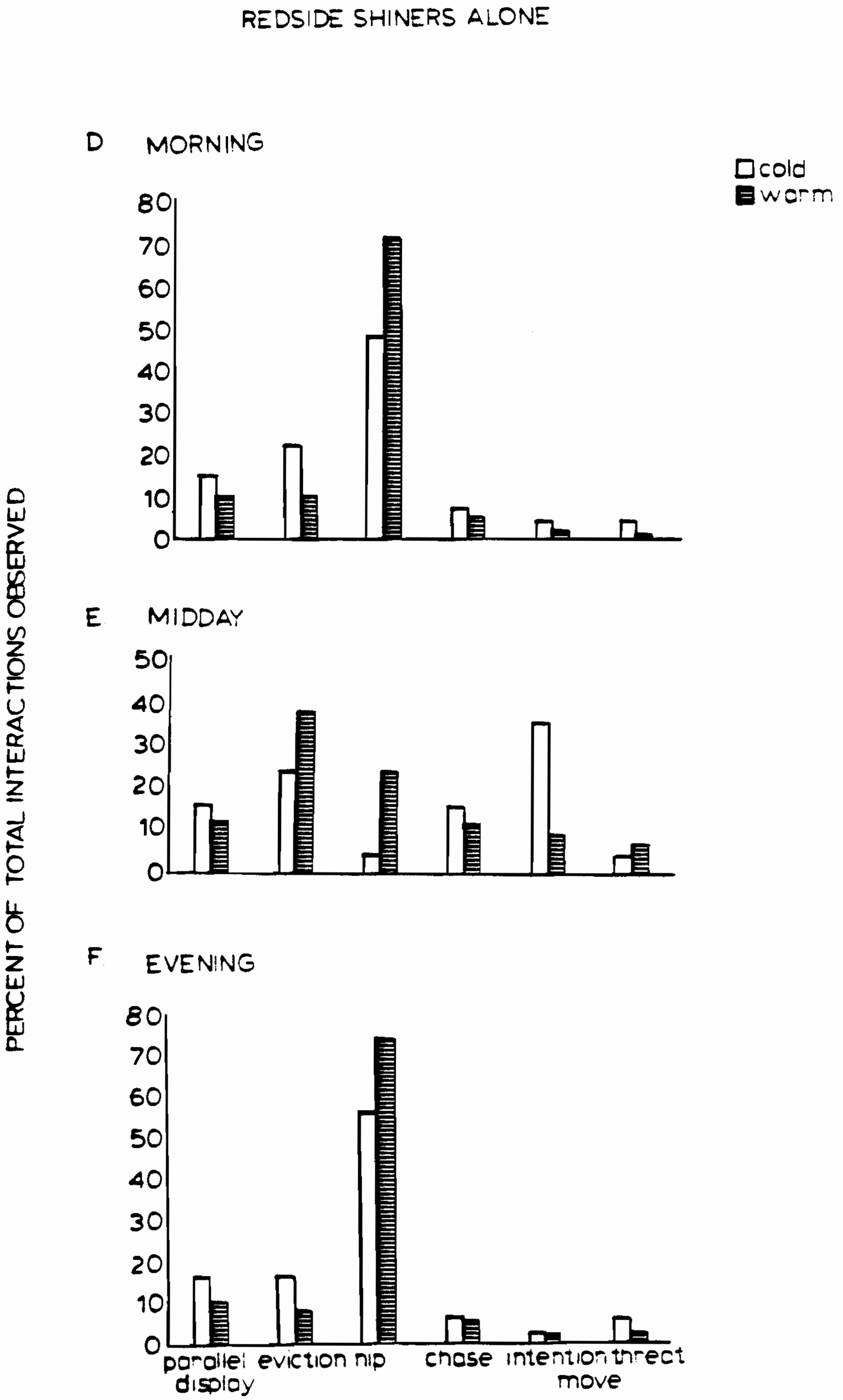

Fig. 10. continued

at cold temperatures when intention moves were the largest percentage (36%)(Fig. 10E). The total number of interactions observed, 25, during this time was small relative to other times and other conditions (Table 5). Interactions were generally more intense during feeding periods than during non-feeding periods. Body movements were more exaggerated and occurred at more rapid rates and greater distances were covered in an interaction.

DISCUSSION

The social behavior of the redside shiner is diverse and complex, but highly plastic. At cold water temperatures and in the presence of steelhead trout, shiners formed loose aggregations in which intraspecific interactions were minimal. At more favorable conditions, warm temperatures or absence of steelhead trout at cold temperatures, a portion of the population defended areas on riffles and the remaining fish either moved about individually or in small groups of 3-4 fish, or formed loose aggregations on the back of riffles or at the head of pools. In general, larger fish were most successful in defending area on riffles, where more food was available than in pools. It appears that the ability to adjust its social behavior is an important factor responsible for the ecological success of the redside shiner.

We have observed both types of social organization and most of the behavior types in natural streams. For example, at a water temperature of 23°C on the Applegate River, a tributary of the Rogue River in southwestern Oregon, we observed larger shiners holding station and feeding on invertebrate drift in the water column along with juvenile steelhead trout and chinook salmon (_O. tshawytscha_). Numerous other shiners were observed in loose aggregations in deeper, slower water on the stream margin. We also observed mixed groups of shiners and chinook salmon moving actively about in deep pools. Changes in social organization under different environmental conditions have been reported for coho (Mason and

Chapman 1965) and chinook salmon (Reimers 1968). Kawanabe (1969) reported that the social organization of the ayu (Plecoglossus altivelis), a stream dwelling salmonid, varied with food abundance. The ayu formed schools when algae, the primary food of adults, was abundant. When algae was scarce, the ayu was territorial.

Aggregations formed by redside shiners were loosely structured. Larger fish tended to be near the front of a group and dominated smaller fish in most encounters. There did not appear to be a dominance hierarchy within the group nor was there a clearly dominant individual or individuals as has been observed in hierarchies of juvenile coho salmon (Mason and Chapman 1965; Hartman 1965).

Dominance in intraspecific interactions between redside shiners was apparently determined by size of the individual and by proprietorship of an area. Larger fish generally prevailed in encounters between different sized individuals. In contests between fish of the same size, proprietors generally prevailed. Size, proprietorship, and coloration have been identified as characteristics of dominant individuals in intraspecific interactions between juvenile salmonids (Keenleyside and Yamamoto 1962; Chapman 1962; Reimers 1968).

Number, type, and intensity of intraspecific interactions by redside shiners were influenced by the presence of food. Most interactions were observed during feeding periods. Nips, which we consider to be one of the more aggressive acts in the behavioral repertoire of the shiner, were the most frequent behavior observed during feeding periods. During non-feeding periods, number of interactions decreased; less aggressive acts such as evictions and intention moves were most common then. Similar changes in activity were noted in the field between morning and midday and midday and evening when shiners were observed alone at warm water temperatures. When steelhead trout were present at cooler water temperatures in the field, shiners were most active at midday when trout were less active (Reeves et al. in prep). Shiners were much less active in the morning and the evening, when trout were most active. This response to food availability may allow the shiner to reduce energy expenditures when food decreases.

The plastic social behavior of the redside shiner appears to be responsible to a large degree for its ecological success. We believe that more detailed studies of the redside shiner and other non-game fish would provide valuable insights into the ecological adaptation and competitive nature of these species.

CONCLUSIONS

Interactions between redside shiners and juvenile steelhead trout were influenced by water temperature. Trout prevailed, by interference competition, at cool temperatures and shiners dominated, by exploitation competition, at warm temperatures.

In unfavorable conditions, the response of each species to the other varied. At warm temperatures, steelhead trout in the presence of redside shiners attempted to maintain territories in the laboratory streams. Only a single trout was able to successfully maintain a suitable territory; all others migrated from the channel. In the field, we observed steelhead trout and chinook salmon early in the year in the area were I made the observations of shiners in allopatry. I did not observe any interactions between shiners and salmonids in that area but by mid-summer when water temperatures began to rise, no salmonids were observed in the study area and shiners were abundant.

At cool temperatures, shiners utilized different habitats and adjusted their behavior in response to the dominance of steelhead trout. In the presence of trout, shiners were found in deep, slow areas but foraged in areas of faster current velocities, that were inhabited by steelhead trout, at times of the day when food availability was low and trout were least aggressive. Shiners were also active at night; they appeared to feed on benthic organisms at this time. When trout were absent at cool temperatures and at warm temperatures when trout were present or absent, shiners inhabited the same types of habitats as did trout and were not active at night.

Under unfavorable conditions, the social organization of the redside shiner also changed. In the presence of steelhead trout at cool temperatures, shiners formed loose aggregations with few intraspecific interactions between individuals. Under other conditions, shiners were territorial and exhibited high levels of intraspecific aggression. The plasticity of the shiner's behavior allowed it to remain in the system during less favorable conditions. The behavior of the trout was more rigid and they left the system during less favorable conditions.

Werner (Kerr and Werner 1980) believed that niche shifts by competing species of fish could not be explained on the basis of physiological differences between the species. Baltz et al. (1982) found that the outcome of competition for cover between two fish species was related to the metabolic performance of the species at a given water temperature. The species that prevailed was the one least stressed at the given temperature. In the present study, I believe one species was able to dominate under a given temperature regime because it was better adapted metabolically. I did not determine the scope for activity (Fry 1947) of each species but I surmise that the scope for activity of the steelhead trout was greater than that of the redside shiner at cool water temperatures and the opposite true at warm temperatures.

Disease confounded the effects of water temperature on interactions between the two species but to an unknown extent at the present time. The susceptibility of each species to _F. columnaris_ varied with water temperature and the abundance of the other species. This should provide a starting point for future research. Moore (1983) emphasized the need to consider the effects of disease and parasites on fundamental processes such as competition and prey selection.

Results from this study have important implications for fishery and land management. First, I believe that we need to evaluate the usefulness of programs designed to control non-game species, which are often held responsible for the demise of salmonid populations. This study shows that environmental conditions affect the outcome of interactions between redside shiners and steelhead trout. If we want to successfully control non-game fish populations, we should manage streamside habitat throughout the watershed in order to create less favorable conditions for the undesired species and more favorable conditions for salmonids. We should decrease the use of chemical and mechanical controls. Secondly, we need to consider the cumulative impact of land-management practices on the fish community. To date, we have been concerned with the effects of land-management practices on the immediate area while neglecting the impact in areas lower in the watershed.

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Appendices

Appendix I. Preliminary observations of redside shiners and juvenile anadromous salmonids in streams in Western Oregon. All observations were made with mask and snorkel. Species codes are: RS - Redside shiners, SH - Steelhead Trout, ChS - Chinook Salmon, and CoS - Coho Salmon.

Location	Date	Water Temp. (°C)	Species Observed	Habitat	Comments
Rogue River System					
Slate Cr. - near confluence with Applegate River	6/81	17	RS, SH, ChS	Pool	All species in pool but no interactions observed.
Applegate R. - near confluence with Slate Cr.	6/81	20	RS	Pool	RS in large school in pool on margin.
	6/81	20	RS, SH, ChS	Run	All species holding position in current feeding on drift.
Galice Cr. - near confluence with Rogue R.	6/81	14	SH	Pool	No RS in Galice Cr. but were numerous in Rogue R., which was much warmer.
Graves Cr. - 1 km above confluence with Rogue R.	6/81	26	RS, SH	Run	SH in faster water at head of run and RS in large group in deeper, slower water.
	7/81	26	RS	Run	RS abundant throughout run; only 2 SH observed.

Location	Date	Water Temp. (^{o}C)	Species Observed	Habitat	Comments
Graves Cr. - 2 km above confluence with Rogue R.	7/81	26	RS, SH	Pool	RS and SH in mixed group at head of pool.
Graves Cr. - 9 km above confluence with Rogue R.	7/81	27	RS	Pool	RS distributed throughout pool.
	7/81	27	RS	Riffle	RS distributed throughout riffle.
Graves Cr. - 9 km above confluence with Rogue R.	7/82	22	RS, SH	Pool	few adult RS present but young-of-the-year abundant. SH abundant throughout pool.
	7/82	22	SH	Riffle	RS absent and SH abundant.
Graves Cr. - 16 km above confluence with Rogue R.	7/81	26	RS, SH	Riffle	RS distributed throughout riffle. Few SH present were mixed with RS.
Graves Cr. - 16 km above confluence with Rogue R.	7/82	23	RS	Riffle	Few RS and no SH observed.
Graves Cr. - 30 km above confluence with Rogue R.	7/81	26	RS	Riffle	RS distributed throughout riffle. No SH observed.
Graves Cr. - 30 km above confluence with Rogue R.	7/82	24	RS, SH	Riffle	Abundance of both species low.

Location	Date	Water Temp. (^{o}C)	Species Observed	Habitat	Comments
Graves Cr. - 40 km above confluence with Rogue R.; end of county road.	7/81	25	SH	Riffle	Steep gradient with large boulders and cobble.
Illinois R. - from campground at trailhead downstream 1.5 km.	7/81	23	SH	Riffles Pools	
W. Fork Illinois R. - near Rt. 199.	6/81	18	RS, ChS	Pools	Both species observed swimming together in single pool.
E. Fork Illinois R. - above confluence with W. Fork.	6/81	19	RS, SH	Riffles	Both species distributed throughout riffles.
Elk Cr. - near Rt. 199.	6/81	12	SH	Riffle	Only fish observed were recently emerged SH.
<u>Siuslaw River System</u>					
Indian Cr. - above confluence with Siuslaw R.	7/81	16	RS, SH, ChS, CoS	Pool	All species distributed throughout pool. No interactions observed.
Siuslaw R. - above confluence with Indian Cr.	7/81	19	RS	Run	No salmonids observed.

Location	Date	Water Temp. (^oC)	Species Observed	Habitat	Comments
<u>Millicoma River System</u>					
E. Fork of Millicoma R. - at Myrtle Grove State Wayside.	7/81	16	RS, SH ChS, CoS	Run	All species distributed throughout run. RS and ChS also in deeper, slower pools.
E. Fork of Millicoma R. - at Myrtle Grove State Wayside.	9/81	15	RS, SH ChS, CoS	Run	All species distributed throughout run.
E. Fork of Millicoma R. - at Myrtle Grove State Wayside.	5/82	not taken	RS, SH ChS, CoS	Run	SH in fastest water. RS and ChS at back of run near pool.
E. Fork of Millicoma R. - at confluence with Glenn Cr.	7/81	21	RS, SH, CoS	Pool	SH at head of pool and RS and CoS in back in slower water. Salmonids fed on drift and RS on bottom. No interspecific interactions observed.
E. Fork of Millicoma R. - at confluence with Glenn Cr.	9/81	16	SH, CoS	Pool	No RS observed.
E. Fork of Millicoma R. - at confluence with Glenn Cr.	5/82	16	RS, SH, CoS	Pool	Same pattern of distribution that was observed in 7/81.

Location	Date	Water Temp. (°C)	Species Observed	Habitat	Comments
Glenn Cr. - above confluence with E. Fork of Millicoma R.	7/81	11	SH, CoS	Pool	No RS observed in Glenn Cr. but were abundant in E. Fork of Millicoma River.
Glenn Cr. - 1.5 km above confluence with E. Fork of Millicoma R.	7/81	11	SH, CoS	Pool	No RS observed.
Glenn Cr. - 1.5 km above confluence with E. Fork of Millicoma R.	9/81	17	SH, CoS	Pool	No RS observed.
Glenn Cr. - 1.5 km above confluence with E. Fork of Millicoma R.	5/82	14	SH, CoS	Pool	No RS observed. Largest salmonids in fastest water.
<u>Smith River System</u>					
Vincent Cr. - above confluence with Smith R.	7/81	16	RS, SH, CoS	Pool	SH at head of pool and RS and CoS in back in slower water. Salmonids fed on drift and RS on bottom. No interspecific interactions observed.
Vincent Cr. - pools created by Bureau of Land Management.	7/81	16	RS, CoS	Pool	Density of both species low.

Location	Date	Water Temp. (°C)	Species Observed	Habitat	Comments
Umpqua River System					
Cow Cr. - power substation upstream from Riddle, OR.	7/81	23	RS	Pools Runs	RS abundant throughout area. Smallmouth bass (Micropterus salmoides) also present.
Cow Cr. - 6 km above power substation.	7/81	23	RS, SH	Riffle	RS abundant. Only a few SH observed; may have been hatchery rainbow trout
Cow Cr. - 6 km above power substation.	9/81	17	RS, SH	Riffle	RS abundant.
Cow Cr. - 6 km above power substation.	5/82	16	RS, SH ChS	Riffle	RS abundant and in spawning colors. Only a few salmonids observed.
Cow Cr. - 6 km above power substation.	7/82	21	RS, SH ChS	Riffle	Only a few RS adults observed but young of the year were abundant along margins. 3-4 SH and 2 hatchery rainbow trout also observed.
Cow Cr. - 9 km above power substation.	7/81	24	RS, SH	Pool	RS abundant. Only a few SH observed; may have been hatchery rainbow trout.

Location	Date	Water Temp. (°C)	Species Observed	Habitat	Comments
Cow Cr. - 9 km above power substation.	9/81	18	RS	Pool	RS abundant. No salmonids observed.
Cow Cr. - 9 km above power substation.	5/82	16	RS	Pool	Only a few adult RS observed.
Cow Cr. - 15 km above power substation.	7/81	24	RS	Pools	RS abundant. Only a few salmonids observed. Area heavily impacted by dredge mining.
	7/81	24	RS	Riffles	RS abundant. Only a few salmonids observed. Area heavily impacted by dredge mining.
Cow Cr. - 32 km above power substation, near railroad bridge.	7/81	25	RS, SH	Run	RS abundant. Only a few salmonids observed.
Steamboat Cr. - below confluence with Canton Cr.	7/81	24	RS, SH	Run	SH in faster areas and RS in slower areas along margins.
Steamboat Cr. - below confluence with Canton Cr.	9/81	16	RS, SH	Run	SH in faster areas and RS in slower areas along margins.

Location	Date	Water Temp. (^oC)	Species Observed	Habitat	Comments
Steamboat Cr. - below confluence with Canton Cr.	5/82	15	RS, SH	Run	SH in faster areas and SH in slower areas along margins.
Steamboat Cr. - 1.5 km above confluence with Canton Cr.	7/81	21	RS, SH	Pool	Only 2 RS observed.
Steamboat Cr. - 1.5 km above confluence with Canton Cr.	5/82	16	RS, SH	Pool	SH in faster water at head of pool. RS in slower water along margins.
Canton Cr. - various locations	7/81 - 7/83		SH	All	RS were never observed in Canton Cr. or any other tributaries of Steamboat Cr.

Appendix II. Production of redside shiners and steelhead trout ($\geq 1^+$) at different temperatures in laboratory stream channels. Trials with only redside shiners and only steelhead trout are referred to as RS and SH, respectively. Trials with both species present are designated RS-SH.

		Initial Conditions				Final Conditions																
						Residents				Migrants					Unrecovered							
		No. of Fish	Biomass (g)	Mean Wt. (g)	±1 SD	No. of Fish	Biomass (g)	Mean Wt. (g)	±1 SD	No. of Fish	Day	Biomass (g)	Mean Wt. (g)	±1 SD	No. of Fish	Est. Biomass (g)	Mean Wt. (g)	±1 SD	Total Biomass (g)	Estimated Production (g)	Date
(1) Steelhead Trout																					
SH																					
Temperature (°C)																					
12.0-15.0		6	47.4	7.90	2.76	6	56.4	8.97	2.78	0					0				56.4	9.0	June 1983
19.0-22.0		4	29.0	7.25	2.54	3	23.9	7.97	2.37	1	1	8.4	8.40		0				32.3	3.3	June 1983
RS-SH																					
Temperature (°C)																					
12.0-15.0	I.	5	50.9	10.18	2.18	5	59.9	11.98	2.82	0					0				59.9	9.0	Aug. 1983
	II.	5	55.2	11.24	1.79	4	52.2	13.10	1.51	1	9	12.1	12.12		0				64.3	9.1	Oct. 1983
19.0-22.0	I.	5	42.8	8.56	2.78	1	10.5	10.52		3	1-3	23.0	7.67	2.80	1	11.6	11.58		45.1	2.3	Aug. 1983
	II.	4	41.5	10.38	4.09	1	7.8	7.8		3	1-3	34.8	11.60	4.95	0				42.6	1.1	Oct. 1983
(2) Redside Shiners																					
RS																					
Temperature (°C)																					
12.0-15.0		28	154.4	5.51	2.26	28	160.7	5.79	2.26	0					0				160.7	6.3	Sept. 1983
19.0-22.0		27	149.1	5.52	2.01	17	101.3	5.96	2.21	8	1-13	52.5	6.56	1.86	2	4.7	2.35	0.49	158.5	9.4	Sept. 1983
RS-SH																					
Temperature (°C)																					
12.0-15.0	I.	38	182.7	4.80	2.06	26	124.7	4.80	1.38	10	1-11	42.7	4.27	1.38	2	14.2	7.10	6.30	181.6	-1.1	Aug. 1983
	II.	33	177.4	5.38	2.29	24	125.1	5.21	2.23	7	1-11	42.9	6.13	1.99	2	4.5	2.25	0.95	172.5	-4.9	Oct. 1983
19.0-22.0	I.	25	115.0	4.63	1.32	16	87.2	5.45	1.42	6	1-3	31.4	5.23	1.42	2	6.5	3.24	1.05	125.1	9.3	Aug. 1983
	II.	25	148.1	5.92	2.19	19	120.1	6.32	2.65	4	1-11	27.5	6.87	1.60	2	10.2	5.25	4.43	157.8	9.2	Oct. 1983