Predation Risk and the Importance of Cover for Juvenile Rainbow Trout in Lentic Systems

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Abstract.—Juvenile rainbow trout *Oncorhynchus mykiss* stocked in midelevation reservoirs in Utah inhabit shallow nearshore areas and are vulnerable to predation from piscivorous fish and birds. We determined the use and importance of nearshore habitats by (1) measuring habitat selection by, prey availability to, and feeding of juvenile rainbow trout in two reservoirs with populations of predators, and (2) measuring survival and growth rates in the presence and absence of cover in a pond experiment where adult brown trout *Salmo trutta* were predators. In the reservoirs juvenile rainbow trout (60–120 mm standard length) were abundant in complex inshore habitats but avoided simple habitats such as sand and gravel during the day. At night, however, juvenile rainbow trout in both reservoirs were observed in more exposed areas, and they rested on the bottom. Measurements of gut fullness indicated that juvenile rainbow trout fed actively on large *Daphnia* spp. during the day but little at night. Because large daphnia were usually more abundant offshore than inshore in both reservoirs, selection of inshore cover is believed to be primarily a response to greater predation risk offshore. In the pond experiment, the presence of brown trout significantly increased mortality of juvenile rainbow trout, decreased their growth rates, and caused them to avoid open-water areas. The presence of cover significantly decreased predation rates but did not affect growth of the juvenile rainbow trout. Fisheries managers should consider augmenting cover in reservoirs and lakes where juvenile trout are stocked to minimize losses of trout to predators.

To avoid predation, fish often move to structurally complex habitats where predators cannot forage effectively (Glass 1971; Savino and Stein 1982). Because of this, complex habitats that provide cover are often important nursery areas for the young of many fish species (Hall and Werner 1977; Orth et al. 1984; Lowe-McConnell 1987), and this cover may appreciably increase the survival of juvenile fish (Shulman 1985; Werner and Hall 1988). In lentic systems, juvenile fish often require structurally complex habitats such as aquatic macrophyte beds (Hall and Werner 1977; Mittelbach 1986), inundated vegetation (Aggus and Elliot 1975), and large boulders (Trendall 1988).

Wild populations of lake-dwelling rainbow trout *Oncorhynchus mykiss* normally have nursery areas in small streams and emigrate to lakes after growing for 1–3 years in the streams (Kwain 1983).

In contrast, juvenile rainbow trout stocked directly into lakes or reservoirs must contend immediately with lacustrine predators. These juvenile fish frequently inhabit the littoral zones until they reach standard lengths (SL) of 100–120 mm, when they move offshore to the limnetic zone (unpublished data).

Although many diurnally active fish in temperate lakes inhabit complex habitats, most of these fish shift from a daytime feeding area near cover to a nighttime resting area on the bottom in relatively exposed locations (Emery 1973; Helfman 1981). Others have a strong affinity for shelter sites at night (Helfman 1981). In many lentic systems, adult brown trout *Salmo trutta* are nocturnally active (Eriksson 1978; Oswald 1978) and may be important predators of juvenile rainbow trout (Sharpe 1957; Wales and German 1956; our unpublished data). Because of the presence of nocturnal brown trout as well as diurnal predators (e.g., piscivorous birds and adult cutthroat trout *Oncorhynchus clarki*), juvenile rainbow trout may select both day and night habitats that provide cover. Little is known, however, about their use

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of cover by juvenile rainbow trout in lentic systems or about its importance in reducing predation.

To examine the use of cover by rainbow trout, we measured diurnal and nocturnal habitat selection in two Utah reservoirs that had fish and bird predators. We also monitored the abundance of zooplankton prey at inshore and offshore sites, and we determined temporal variations in feeding to assess the relative importance of different areas and feeding times for foraging. Because the juvenile rainbow trout in the reservoirs selected inshore, complex habitats, we conducted a controlled pond experiment to test how cover and the presence of predators affected survival and growth of the fish.

Study Sites

We studied the behavior of juvenile rainbow trout in two northern, midelevation Utah reservoirs. East Canyon Reservoir is a 277-hectare impoundment with coordinates 40°54'20"N, 111°35'20"W and an elevation of 1,734 m. It has a mean depth of 23 m and 16 km of shoreline. The littoral zone consists primarily of small substrates (1–20 mm in diameter) such as sand and gravel, with some patches of boulders and inundated terrestrial vegetation but few aquatic macrophytes. East Canyon Reservoir is eutrophic, with an abundant population of large *Daphnia* spp. that provides sufficient forage for juvenile rainbow trout to grow at or near their maximal rate (Marine et al. 1986). The Utah Division of Wildlife Resources stocks the reservoir in early May with 300,000 rainbow trout (mean weight, 6 g; SL, approximately 70 mm). Juvenile rainbow trout are preyed on by brown trout, cutthroat trout, and adult rainbow trout (W. A. Wurtsbaugh, unpublished data), as well as by piscivorous birds such as western grebes *Aechmophorus occidentalis*, Forster's terns *Sterna forsteri*, and common mergansers *Mergus merganser*. Redside shiners *Richardsonius balteatus*, kokanee *Oncorhynchus nerka*, Utah suckers *Catostomus ardens*, speckled dace *Rhinichthys osculus*, and fathead minnows *Pimephales promelas* are also present in the reservoir.

Mesotrophic Causey Reservoir, the second field site, has an area of 58 hectares, coordinates of 41°17'55"N, 111°35'13"W and an elevation of 1,735 m. Its mean depth is 20 m, and its shoreline length is 11.8 km. The littoral zone is similar to that of East Canyon Reservoir except for more medium-sized substrates such as cobble. Because

of the steepness of the shore, the littoral zone is generally less extensive than that in East Canyon Reservoir. Zooplankton is abundant, but densities of large daphnia usually are lower than in East Canyon Reservoir. On 6 June 1988, the Utah Division of Wildlife Resources stocked 30,000 rainbow trout averaging 3.2 g and approximately 60 mm SL in Causey Reservoir as well as 22,300 larger fish (8.2 g, 77 mm). On 15 May 1989, an additional 61,000 rainbow trout (5.7 g, 70 mm) were stocked. In Causey Reservoir, juvenile rainbow trout are vulnerable to predation from adult brown trout, cutthroat trout, and brook trout *Salvelinus fontinalis*. However, unlike at East Canyon Reservoir, few piscivorous birds have been observed at Causey Reservoir. Mottled sculpin *Cottus bairdi* are also present in Causey Reservoir.

Methods

Field studies.—Habitat selection by juvenile rainbow trout in nearshore areas was determined through direct observation along shoreline transects. Sampling began 1 week after the fish were introduced to allow them to acclimate and disperse from the stocking site. Transects were surveyed during the next 4 weeks, when the fish ranged from approximately 60 to 120 mm SL. Because stocked rainbow trout dispersed slowly around the reservoirs (Wurtsbaugh, unpublished data), the transects were confined to within 3 km of the stocking site, which resulted in 48% of the shoreline in East Canyon Reservoir and 36% in Causey Reservoir being surveyed. Within these sampling areas, locations of individual transects were chosen by randomly selecting shoreline sections from a map. At the beginning of the study in 1988, 30-m transects were used in East Canyon Reservoir; later, 100-m transects were used. The length of each transect was measured by a swimmer tied to one end of a 30- or a 100-m rope whose other end was attached to an anchored boat. Forty-three transects (27 in 1988, 16 in 1989) were surveyed in East Canyon Reservoir and 44 (22 in 1988 and 22 in 1989) in Causey Reservoir. Sixty-five percent of the transects were surveyed during day and 35% at night.

Observations of juvenile rainbow trout and their habitats were made by a swimmer, equipped with snorkel and mask, swimming at the surface 1–6 m from the shoreline, where the depth varied from 0 to 2.5 m. Preliminary transects with scuba were made at depths of 2.5 and 6 m, but because no juvenile rainbow trout were seen there, we swam only along surface transects in 1988 and 1989.

Fish beneath the swimmer or between the swimmer and shore could easily be counted unless they were under a rock. Rainbow trout more than 3–4 m offshore from the swimmer probably were not seen. At night, observations were made with an underwater flashlight. The periphery of the light beam was used to observe juvenile rainbow trout because it did not appear to affect their behavior. Observations consisted of counting fish and noting the closest habitat type to each fish. Observations of schooling activity, feeding activity, and distance from substrate were also recorded.

Habitat characteristics were measured by the swimmer while swimming back to the boat. At every mark on the measuring rope (5-m intervals for 100-m transects, 2-m intervals for 30-m transects) the percentages of different habitat types within a 1-m-diameter circle were estimated. Habitat was classified into seven categories: bed-rock, sand-mud (sediment size, <2 mm), gravel (2–20 mm), cobble (20–200 mm), small boulders (200–500 mm), large boulders (>500 mm), and inundated vegetation.

Selectivity for each substrate type was calculated with Manly's α (Manly 1974):

$$\alpha_i = \frac{r_i/n_i}{\sum_{i=1}^k r_i/n_i};$$

r_i is the proportion of fish associated with habitat i , n_i is the proportion of habitat type i in the environment, and k is the total number of habitat categories. Random use of habitat types occurs when $\alpha_i = 1/k$. Significant differences in habitat selection within time periods were tested with a chi-square (χ^2) goodness-of-fit test (Manly 1974).

To determine if juvenile rainbow trout inhabited nearshore areas because of prey availability, we compared the abundance of daphnia (the principal prey of juvenile rainbow trout in both reservoirs) in nearshore and offshore areas. Daphnia biomass at the offshore sites was a measure of food available to juvenile rainbow trout if they moved to the limnetic zone where cover was low and predation risk high. Food available to juvenile rainbow trout was estimated from the biomass of daphnia 1.0 mm or more in length, which included 93% of all daphnids found in juvenile rainbow trout stomachs.

In 1989 zooplankton were collected periodically in both reservoirs for 2 months after juvenile rainbow trout were stocked. Vertical zooplankton tows were made near the stocking sites with a 30-cm-

diameter plankton net (153- μ m mesh). We calculated daphnia densities by assuming that the net was 100% efficient, but this may have underestimated actual densities because nets are frequently less than 50% efficient in eutrophic waters (APHA et al. 1985). Inshore samples were taken from the bottom to the surface at places where the depth was 1.5 m (3–4 m from shore). This depth represents the approximate mean depth where juvenile rainbow trout were observed during shoreline transects in the littoral zone. In Causey Reservoir, the offshore site was at a depth of 10 m (approximately 20 m from shore). In East Canyon Reservoir, offshore sites were at depths of 10 m and 45 m (some 20 and 200 m from shore). Only the upper 5 m were sampled at the offshore sites because rainbow trout remained primarily in the epilimnion when they moved offshore (our unpublished data). Two or three replicate samples were taken on each date at each site. The first 50–100 daphnia encountered in each sample were measured to the nearest 0.03 mm from the top of the head to the base of the tail spine with an ocular micrometer. Dry weights (W , mg) of individual daphnids were calculated from lengths (L , mm) with formulas adapted from McCauley (1984): (1) *D. galeata*, $\log_e W = -4.83 + 2.53 \log_e L$; (2) *D. schodleri* and *D. pulex*, $\log_e W = -5.04 + 2.83 \log_e L$.

We analyzed diel feeding activity of juvenile rainbow trout to determine how it was related to diurnal and nocturnal habitat use. Juvenile rainbow trout were sampled in 1989 at each reservoir after the fish had been present for 7–10 d and again after 17–21 d. We sampled 10–12 fish approximately every 3 h for 24 h. All fish were sampled within 10 m of shore with a 23-m beach seine, a boat-mounted electrofishing unit, dip nets, or gill nets set for 5–10-min intervals. Within 5–20 min of capture, fish were immobilized with tricaine (MS-222), weighed to the nearest 0.1 g, and measured to the nearest millimeter. Stomachs were removed and placed in 95% ethyl alcohol. Stomachs were visually inspected to estimate the relative volumetric composition of prey taxa, dried for 18 h at 60°C, and weighed to the nearest 0.0001 g dry weight (DW). A gut-fullness index (GFI; Wurtsbaugh and Li 1985) was calculated as

$$\text{GFI} = \frac{100,000(\text{DW gut contents, mg})}{(\text{fish SL, mm})^{3.05}}.$$

The exponent 3.05 was empirically derived from the standard length–wet weight regression of ju-

venile rainbow trout in both reservoirs. Values of GFI observed in the rainbow trout ranged from 0.0 to 11.6.

Pond experiment.—We tested the effect of predators and cover on the survival, growth, and behavior of juvenile rainbow trout with a controlled pond experiment during June 1988. The pond was circular with a flat bottom and a maximum depth of 1.4 m. After the pond was drained and all vegetation and debris were removed, the pond was divided with small-mesh netting (2.5 m in height; 7-mm-square mesh) into eight equal pie-shaped sections, each with an area of 200 m². A continuous flow of water was maintained with four inlet pipes placed evenly around the pond. Each section received a flow of approximately 30 L/min. Surface temperatures in the pond ranged from 15°C at the start to 21.5°C at the end of the experiment. The bottom temperature was 17°C at the end of the experiment. These temperatures were near the preferred temperature range of juvenile rainbow trout in East Canyon Reservoir (16–20°C; Wurtsbaugh, unpublished data).

Survival, growth, and behavior of juvenile rainbow trout were tested in a 2 × 2 factorial design, with the presence and absence of predators and the presence and absence of cover as the treatments. Each treatment was duplicated and assigned randomly to sections of the pond. To simulate complex habitats available in the two reservoirs, three types of cover were used in each section that received cover: (1) 250 wooden stakes (1.0 and 0.5 m high) placed in a grid 4–6 cm apart; (2) 30 cement cinder blocks stacked in a loose rectangular configuration; and (3) 12 inverted laundry baskets (0.1 m³) with 4-cm-square mesh. The total area of cover within each pond section was approximately 16 m². Cover extended from near shore (depth, 0.5 m) to a depth of 1.2 m to ensure that cover was available in areas with suitable temperatures.

Brown trout and juvenile rainbow trout were obtained from hatcheries of the Utah Division of Wildlife Resources. Brown trout (295–420 mm SL) from hatchery brood stock were used as predators; they become piscivorous at lengths greater than 250 mm SL (Scott and Crossman 1973; Garman and Nielsen 1982). For 2 weeks before the experiments began, the brown trout were held in a raceway and fed juvenile rainbow trout.

At the start of the experiment, 180 juvenile rainbow trout were put in each section. Groups of 20–50 fish were counted and stocked sequentially around the pond in each section. To estimate the

initial mean weight of the juvenile rainbow trout in the experiment, 20% of the fish from each group were randomly selected and weighed to the nearest 0.1 g. The estimated mean individual weight of these fish was 4.2 g (range, 3.0–7.0 g). The following day adult brown trout were weighed (mean weight, 875 g; range, 410–1,680 g; $N = 44$), and 11 fish were stocked into each of the four sections such that each section received similar sizes of fish. Total predator weight for each section was within 5% of the other sections. At the end of the experiment all brown trout were recovered and appeared in good condition.

Behavioral observations were made during the main experiment and during a preliminary experiment. We stood 8–12 m from a study section and observed the fish with binoculars equipped with polarizing filters. The location of juvenile rainbow trout was determined before and after the addition of brown trout predators. The proportions of trout visible within 3 m of shore (inshore) and greater than 3 m from shore (offshore) were estimated. Fish offshore in water deeper than approximately 35 cm could not be observed. For each section, observations were made seven times at various times during daylight.

After 10 d the pond was partially drained and brown trout were removed with a large-mesh seine. The pond was then drained further until a small-mesh net could be used to remove the majority of juvenile rainbow trout. Finally, the pond was completely drained to collect the remaining fish. The rainbow trout removed from the pond were counted, and 50 from each section were randomly selected and weighed. During the final draining a few juvenile rainbow trout escaped from one section. The total number of fish remaining in this section was estimated by adding the number of juvenile rainbow trout captured with the seine to the number of fish estimated to have avoided the seine net (based on the mean seining efficiency rate of 81% [range, 64–95%] in the other sections).

Growth and mortality were analyzed with a fixed-effects model of a two-way analysis of variance. Growth was analyzed as the percent increase in weight. Mortality was analyzed as the number of juvenile rainbow trout lost during the 11-d experiment.

Results

Field Studies

During the day, juvenile rainbow trout that were in the littoral zone of both reservoirs occupied habitat types in a nonrandom pattern (Causey

FIGURE 1.—Mean ($\pm$ SE, vertical line) selectivity values (Manly's α) for habitat types used by juvenile rainbow trout during the day (A, B) and night (C, D) in East Canyon Reservoir (19–25 May 1988 and 16–31 May 1989) and Caussey Reservoir (17 June–12 July 1988 and 31 May–19 June 1989), Utah. The dashed lines indicate the level of selectivity if all habitat types were used at random. Habitat complexity increases from left to right: sand (S); gravel (G); cobble (C); bedrock (BR); small boulders (SB); large boulders (LB); inundated vegetation (V). Number of rainbow trout sampled (n) is also indicated. The actual numbers of fish observed in each habitat and the percentages of each habitat available are given in Tabor (1990).

Reservoir, $\chi^2 = 1,113.9$, $df = 6$, $P < 0.001$; East Canyon Reservoir, $\chi^2 = 892.1$, $df = 6$, $P < 0.001$. They selected the most structurally complex habitats (large boulders, inundated vegetation, and small boulders) and avoided other substrates such as sand and gravel (Figure 1A, B). Although aquatic macrophytes were rare in the reservoirs, and thus poorly sampled, we saw no juvenile rainbow trout in aquatic macrophytes, a finding similar to that of Wasowicz (1991). Although many juvenile rainbow trout were observed closest to sand and gravel substrates, these fish were often near more complex escape cover. Because we recorded the habitat closest to the fish, the actual use of complex habitat may have been underestimated. Al-

though boulders and inundated vegetation combined made up approximately 20% of the nearshore habitat, most of these elements were in small patches scattered along the shore. Juvenile rainbow trout did not use the small patches; rather, they preferred to be on the offshore side of large patches of boulders, inundated willows *Salix* sp., and fallen trees.

During the day, juvenile rainbow trout were observed from a few centimeters to 2 m above the substrate. Usually they were observed in schools by themselves or occasionally in schools with red-side shiners. Fish near cover were usually in loose aggregations and not strongly oriented to one another. When fish were observed away from cover,

they were usually in schools of more than 30 fish and appeared to be strongly oriented to one another.

In both reservoirs, nighttime habitat use by juvenile rainbow trout differed from daytime use. The fish did not strongly select structurally complex habitats at night and were often found in exposed areas such as sand, gravel, and cobble (Figure 1C, D). They occupied habitat types at night in a nonrandom pattern (Causey Reservoir, $\chi^2 = 112.3$, $df = 6$, $P < 0.001$; East Canyon Reservoir, $\chi^2 = 23.3$, $df = 6$, $P < 0.001$). Only bedrock appeared to be strongly avoided, possibly due to its steep slope. Fish observed at night had descended from the water column to within 10 cm of the substrate. They were easily approached and were motionless or "resting." No feeding or schooling activity was detected. At night, juvenile rainbow trout often were distributed evenly along the transects. For example, in a nighttime survey of Causey Reservoir, we found 290 juvenile rainbow trout distributed along a 200-m shoreline section composed primarily of gravel and cobble except for a 10-m section of large boulders. In contrast, during the day we observed 305 fish along the same section but they were all within the narrow section of large boulders.

Daphnia located offshore were usually larger and accounted for more biomass than daphnia found inshore in both reservoirs (Figure 2). The abundance of daphnia in the littoral zone was low when trout were stocked, but numbers increased greatly within 1–2 weeks. Except for a spring pulse of large daphnia close to shore, mean biomass of daphnia was 3–23 times higher 30 m offshore than in the nearshore area of Causey Reservoir. Mean daphnia length from late May to mid-July was 0.95 mm offshore and 0.86 mm in the inshore areas of Causey Reservoir (Tabor 1990). In East Canyon Reservoir the biomass of large daphnia was often much higher 30–200 m offshore than nearshore (Figure 2). Mean daphnia lengths were 1.29 mm (200-m site), 1.23 mm (30-m site), and 1.12 mm (4-m site).

Stomach analyses, as well as underwater observations, demonstrated that juvenile rainbow trout fed actively during the day. During the diel sampling periods, daphnia (primarily *D. pulex* and *D. galeata*) made up more than 99% and 96% of the diet volume of juvenile rainbow trout in East Canyon and Causey reservoirs, respectively. Gut fullness decreased at night, the lowest levels occurring around dawn (Figure 3). In Causey Reservoir, fish began feeding at dawn and gut fullness did not

FIGURE 2.—Dry-weight biomasses ($\pm$ SE, vertical line) of 1-mm or larger daphnia collected at different distances from shore in Causey and East Canyon reservoirs, 1989. Means and standard errors were calculated from two or three vertical net hauls taken at the same site. In Causey Reservoir, the 3-m site was sampled at depths of 0–1.5 m; at the 30-m site, the top 5 m of the water column was sampled. In East Canyon Reservoir, the 4-m site was sampled at 0–1.5 m; at the 30-m and 200-m sites the top 5 m of the water column was sampled. Arrows indicate juvenile rainbow trout stocking dates.

peak until late afternoon (1900 hours) on both sampling days (Figure 3). Although gut fullness of East Canyon Reservoir fish varied between the two sampling periods (Figure 3), feeding occurred mostly during the day and at dusk, and gut fullness declined throughout the night. Peaks in gut fullness in East Canyon Reservoir corresponded to wind events that may have moved large offshore daphnia close to shore. Visual observations and zooplankton samples at another East Canyon Reservoir site indicated that large daphnia were abundant close to shore after wind events.

Pond Experiment

Predaceous brown trout had a highly significant effect on the mortality of juvenile rainbow trout ($F = 574.8$, $df = 1, 4$, $P < 0.001$), which increased approximately sixfold (Figure 4). The presence of

FIGURE 3.—Diel changes in gut fullness of juvenile rainbow trout in Causey and East Canyon reservoirs during the second and third weeks after stocking in 1989. Time of day is given in daylight saving time. Daytime temperatures at 1-m depth during each period are given in parentheses. Two wind events occurred during the sampling at East Canyon Reservoir: on 9 May from 1700 to 1730 hours and on 18 May from 0900 to 1900 hours. Mean standard lengths of juvenile rainbow trout in Causey Reservoir were 78 mm on 25–26 May and 89 mm on 7–8 June. In East Canyon Reservoir, mean lengths were 71 mm on 9–10 May and 76 mm on 18–19 May. Error bars indicate ± 1 SE of the mean.

cover also had a significant effect on the mortality rates of juvenile rainbow trout ($F = 24.0$, $df = 1$, 4 , $P < 0.01$). For predator treatments the probability of mortality was 34% lower in sections with cover than in sections without cover. The interaction of cover and predators on trout mortality was nearly significant ($F = 5.1$, $df = 1$, 4 , $P = 0.09$).

Predation rates in all sections were generally lower than anticipated. Twelve brown trout stomachs (three per section) were examined after the experiment. Three stomachs were empty, four contained snails, six had small amounts of chi-

FIGURE 4.—Effects of brown trout (predator) and cover on the mortality of juvenile rainbow trout during an 11-d pond experiment (3–13 June 1988). Mortality is expressed as the percentage of population lost per day (instantaneous mortality rate; Chapman 1978). The upper ranges of duplicate treatments are indicated by the vertical bars.

ronomids, and one had fish remains. Based on mortality rates, each brown trout consumed an average of only 0.41 trout per day or approximately 0.3% of its body weight. Some cover may have been created at the net margins and lowered predation rates. Although brown trout were observed chasing juvenile rainbow trout on several occasions, they had been habituated to eating pellets at the hatchery, and their limited training with forage fish before the experiment was probably insufficient for them to learn how to effectively pursue and capture prey.

The presence of brown trout predators had a significant negative effect on growth of juvenile rainbow trout ($F = 14.2$, $df = 1$, 4 , $P = 0.02$; Table 1), but the effects of cover and the interaction of cover and predators were not significant ($F = 0.3$, $df = 1$, 4 , $P = 0.59$; $F = 0.8$, $df = 1$, 4 , $P = 0.41$, respectively). Nevertheless, instantaneous growth rates of juvenile rainbow trout in this experiment were high in all sections (mean, 6.2%/d). High growth rates presumably resulted from high food abundance. Large numbers of adult chironomids were observed on the water surface, and the few juvenile rainbow trout stomachs we examined at the end of the experiment contained large numbers of adult and larval chironomids.

The daytime visual observations indicated that brown trout had a significant effect on the distribution of juvenile rainbow trout (Wilcoxon rank-sum test; $P < 0.001$). In sections without preda-

TABLE 1.—Initial and final numbers and wet weights (g) of juvenile rainbow trout (prey) and weights (g) of adult brown trout (predators) used in an 11-d predation experiment (3–13 June 1988).

Treatment	Repli- cate	Prey								Weight increase (%)
		Predator weight		Number		Initial weight		Final weight		
		Mean	SD	Initial	Final	Mean	SE	Mean	SE	
No predators, cover	A			180	171	4.27	0.13	9.06	0.34	112.1
	B			180	173	4.12	0.13	8.66	0.22	115.6
No predators, no cover	A			180	165	4.44	0.14	9.32	0.31	109.7
	B			180	169	4.32	0.14	8.60	0.30	99.0
Predators, cover	A	873	349	180	128	4.34	0.11	7.60	0.20	75.4
	B	879	257	180	134	4.04	0.13	7.80	0.24	93.2
Predators, no cover	A	854	325	180	117	3.86	0.12	6.23	0.20	79.5
	B	902	325	180	118	4.30	0.14	8.32	0.20	93.3

tors, juvenile rainbow trout actively fed at the surface throughout the pond section, and only 22% (± 1 SE, 5%) of the observed fish were inshore. In sections with predators, little feeding activity was detected and 96% (± 1 SE, 4%) of the observed juvenile rainbow trout were inshore in the presence or absence of cover.

Discussion

Results from the pond experiment demonstrated that structurally complex habitats can be used by juvenile rainbow trout to reduce predation. In East Canyon and Causey reservoirs, juvenile rainbow trout selected habitats during the day that could provide escape cover from predators. Diurnal predators (cutthroat trout and piscivorous birds) were present in both reservoirs and were observed pursuing these fish. Therefore, nearshore cover may be important in reducing predation rates in reservoirs and lakes. An increase in juvenile survival may be expected if large patches of boulders or inundated vegetation are abundant along the shoreline. Other studies have also shown that fish recruitment is related to the availability of nearshore cover (Aggus and Elliot 1975; Wright 1990).

Some juvenile fish inhabit nearshore areas in lentic systems because of prey availability (Whiteside et al. 1985) or temperature preference (Wurtsbaugh et al. 1975; Caulton 1978). In both reservoirs, however, prey was both more abundant and larger offshore than inshore, indicating that the inshore areas were inferior for foraging. Similarly, temperature preferences seem unlikely to have caused the fish to select inshore areas, because midday surface temperatures of offshore and inshore areas differed by less than 1°C on the four

dates they were measured in East Canyon Reservoir (Wurtsbaugh, unpublished data).

Consequently, we believe that selection of nearshore cover represents a trade-off between foraging offshore to exploit abundant prey and remaining near cover to lower risk of predation. Studies of bluegills *Lepomis macrochirus* (Werner et al. 1983), blacksmith *Chromis punctipinnis* (Bray 1981), and wrasse *Pseudolabrus celidotus* (Jones 1984) have also demonstrated that juvenile fish inhabit areas that do not maximize foraging but provide sufficient cover from predators.

Juvenile rainbow trout may also maximize foraging opportunities and minimize predation risk by making diel inshore-offshore migrations. In East Canyon Reservoir, we have observed rainbow trout migrating 10–50 m offshore in the morning to feed on abundant large daphnia. After feeding they returned to shoreline areas where risk presumably was reduced (unpublished data).

The change in foraging behavior and the decreased growth rates of juvenile rainbow trout, both due to the presence of brown trout in the pond experiment, suggest that predators may influence rainbow trout food intake. We should caution, however, that the reduced growth of juvenile rainbow trout in the pond sections with predators could have been caused by competition between brown trout and juvenile rainbow trout. We did not document food abundances in the different sections, but the large numbers of chironomids observed in each section indicated high food levels during the experiment. From a controlled predation experiment with juvenile chum salmon *Oncorhynchus keta* and piscivorous coho salmon *O. kisutch*, Hargreaves and LeBrasseur (1986) suggested that reduced growth rates of juvenile chum

salmon were due to intimidation by coho salmon. Reduced food intake due to intimidation by predators has been reported for other fish (Power et al. 1985; Schmitt and Holbrook 1985). Such decreased consumption may reduce growth rates of fish (Werner et al. 1983; Mittelbach 1986). If growth is reduced, juvenile fish will be vulnerable to predators for a longer time and survivorship could be reduced markedly (Werner et al. 1983). In unproductive lentic systems where growth of juvenile rainbow trout is slow and predators are abundant, juvenile rainbow trout may be restricted to the inshore area for extended periods, or they may alter their behavior and accept more risk. Survival of juvenile fish may then be too low to make stocking small rainbow trout of 70 mm SL economically feasible.

Schooling by juvenile rainbow trout also appeared to be influenced by predators and the proximity of cover. Fish near inundated vegetation and large boulders were often numerous but did not appear to be strongly oriented to one another. In contrast, juvenile rainbow trout above small boulders, cobble, and less complex habitats usually occurred in schools. In the pond experiment, schooling appeared to be more pronounced in sections with predators when cover was absent. Thus, schooling by rainbow trout may indicate the presence of predators or a shortage of complex habitats, as has been shown for other species (Shaw 1978; Savino and Stein 1982; Pitcher 1986).

At night, juvenile rainbow trout in both reservoirs rested in exposed areas in a manner similar to other diurnally active freshwater fish (Emery 1973; Helfman 1981). Emery (1973) suggested that fish occupied exposed positions at night because shelter sites were scarce. In our study sites, however, complex habitats had few fish at night; consequently, there was no apparent shortage of shelter sites. In an alternative explanation, Helfman (1981) proposed that temperate freshwater systems generally lack abundant nocturnal predators; thus, prey have little need to seek cover. Although large predaceous brown trout occurred in both reservoirs, they were not abundant. Brown trout may be able to forage under moonlight and starlight (Oswald 1978; Robinson and Tash 1979). In a preliminary laboratory experiment, juvenile rainbow trout used cover extensively at night when a nocturnally active brown trout predator was present, but they occupied exposed areas at night when a predaceous, diurnally active, adult rainbow trout was present (R. A. Tabor, unpublished data). This suggests that juvenile rainbow trout may use cover

extensively when abundant predators are active. Other studies have shown that prey occupy habitats of greater complexity during periods when predators are most active (Hobson 1972; Stein 1979).

For lentic systems in which juvenile rainbow trout are stocked, the augmentation of cover should be considered as a management tool. Inundated vegetation and boulders are particularly valuable habitats. Leaving some inundated trees in new reservoirs may help in this regard. Similarly, Brouha and von Geldern (1979) suggested that planting willows on drawdown zones in western reservoirs would provide cover for juvenile centrarchid fishes. Stocking fish when the water level in the reservoir is at its maximum will usually increase the amount of available cover, because at high water there is usually more inundated vegetation and structural complexity than when the reservoir is drawn down to expose areas where sediments accumulate. For example, in East Canyon Reservoir, inundated vegetation made up 4% of the nearshore habitat during a low-water year (1988), but it made up 12% when water levels were higher (1989). Other studies have shown increases in fish recruitment when reservoirs or lakes have risen and inundated shoreline areas (Aggus and Elliot 1975; Bayley 1977).

Although we demonstrated that juvenile rainbow trout use inshore cover and thereby improve their survival when predators are present, we do not know how much cover is necessary to increase survival. For other species, threshold levels of cover may be necessary (Gotceitas and Colgan 1989), and there may be a positive relationship between the amount of cover and recruitment of juvenile fish (Durocher et al. 1984). The recognition that juvenile rainbow trout in lentic systems rely heavily on littoral cover will, we hope, stimulate additional research on microhabitat selection by this species.

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