

Habitat-dependent interactions between two size-classes of juvenile steelhead in a small stream

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Abstract: The presence of small steelhead (*Oncorhynchus mykiss*; averaging 55 mm fork length) influenced the growth of larger juvenile steelhead (90 mm fork length) during a 6-week experiment conducted in North Fork Caspar Creek, California, in summer 1994. In fenced replicate deep stream sections in this small stream, growth of the larger steelhead was greater in treatments in which small steelhead constituted half of the total biomass of fish than in treatments with an equal biomass comprised entirely of larger fish. In shallow habitats, growth of larger fish was lower in the presence of small fish. The growth of small fish was unaffected by the presence of larger juveniles and also was independent of habitat. Survival of both size-classes was high (70-90%) and unrelated to habitat or the presence of the other size-class. The advantage of large body size in intraspecific interactions among steelhead does not exist in all types of habitat, and interactions between the two size-classes may contribute to lower abundance of large juveniles in streams where aggradation reduces water depth.

Resume : La presence de petites truites arc-en-ciel (*Oncorhynchus mykiss*; d'une longueur moyenne a la fourche de 55 mm) a influe sur la croissance de truites arc-en-ciel juveniles de plus grande taille (longueur a la fourche de 90 mm) au cours d'une experience d'une duree de 6 semaines realisee dans le ruisseau North Fork Caspar en Californie au cours de Fete 1994. Dans des sections jumelees profondes de ce petit ruisseau qui ont ete isolees, la croissance des truites arc-en-ciel de plus grande taille etait plus grande lorsque des petites truites arc-en-ciel constituaient la moitie de la biomasse totale de poissons que lorsqu'on maintenait une biomasse equivalente constituee uniquement de poissons de taille plus grande. Dans les habitats peu profonds, la croissance des poissons de plus grande taille etait plus faible en presence de poissons de petite taille. La croissance des poissons de petite taille n'a pas ete affectee par la presence de juveniles de plus grande taille et etait egalement independante de la profondeur de l'habitat. La survie des deux classes de taille etait elevee (70-90%) et independante de l'habitat ou de la presence de l'autre classe de taille. L'avantage d'une taille corporelle plus grande dans les interactions intraspecifics chez les truites arc-en-ciel ne se manifeste pas dans tous les types d'habitats et les interactions entre les deux classes de taille peuvent contribuer a une abondance plus faible de juveniles de grande taille dans les ruisseaux o^u l'alluvionnement reduit la profondeur de l'eau. [Traduit par la Redaction]

Introduction

Body size strongly influences biotic interactions in fishes. Large body size can provide competitive advantages via greater ability to interfere with other individuals (Grossman 1980a), increased searching capacity (Browman and O'Brien 1992) or capture efficiency (Wanzenbock 1992), or the ability to consume a wider size range of prey (Grossman 1980b). However, smaller animals have lower individual food requirements, so they may be superior competitors in situations where food supply is low (Persson 1985; Hamrin and Persson 1986). Also, although predator-prey relationships among fishes generally favor larger individuals, large fish can experience greater risk of predation from piscivorous birds and mammals (Power 1987; Harvey and Stewart 1991).

Biotic interactions can also be influenced by the physical

structure of the habitat. Predator-prey interactions involving fishes can be altered by elements that affect habitat complexity, such as aquatic vegetation (Eklov and Hamrin 1989; Wahl and Stein 1989) or substrate heterogeneity (Power 1992), as well as by water depth (Harvey and Stewart 1991; Eklov et al. 1994). Less information is available on the dependence of competitive interactions on structural features of the habitat. However, Persson (1987, 1993) showed that interactions between perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) in lentic systems are mediated by access to littoral habitat elements and the presence of piscivorous fish.

In some situations, body size may interact with habitat in mediating interactions among fishes. For several reasons, salmonids in streams may be excellent candidates to exhibit relationships among body size, habitat, and biotic interactions: (i) salmonid fishes often exhibit density-dependent survival and growth (e.g., Grant and Kramer 1990; Crisp 1993); (ii) success in interference competition among salmonids is positively related to body size (e.g., Hughes 1992); (iii) substantial diet overlap among size-classes of salmonids is possible (Allan 1981; Bozek et al. 1994); (iv) predation risk influences salmonid foraging behavior (Dill and Fraser 1984; Angradi 1992); and (v) predation risk is body-size and habitat-depth dependent for stream fishes (Power 1987; Harvey and Stewart 1991).

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The responses of salmonids to changes in habitat may be driven in part by size-dependent biotic interactions. For example, age-0 salmonid density appears to increase following reduction in the frequency of deep habitats and increased primary productivity, while the density of larger fish is reduced or unaffected (Burns 1972; Bisson and Sedell 1984). This pattern may be due in part to competition between size-classes mediated by habitat, because small salmonids may forage effectively in shallow water at the expense of larger fish. In this study, we tested the null hypothesis that survival and growth of juvenile steelhead (*Ohcorhynchus mykiss*) are not affected by interactions between size-classes or by habitat in a small stream. Competition within versus between size-classes was examined by holding biomass constant while comparing survival and growth in single size-class and mixed size-class treatments.

Study site and methods

North Fork Caspar Creek is a small coastal stream in northern California. The 497-ha watershed was logged in the late 1800s and again in 1989-1991. Streamside buffer strips of approximately 50 m, containing redwood (*Sequoia sempervirens*), Douglas-fir (*Pseudotsuga menziesii*), and tan oak (*Lithocarpus densiflora*), were left following the more recent timber harvest. Steelhead were the only fish in the study reach in summer 1994. The stream also contained Pacific giant salamanders (*Dicamptodon tenebrosus*) at a density similar to that of steelhead.

The experiment was conducted in a 1200 m long reach of stream. Discharge at the downstream end of the study reach declined steadily from 0.34 to 0.22 m³·min⁻¹ during the experiment (28 July - 8 September 1994). Water temperatures during the experiment were 11.5-18.5°C at the downstream end of the study reach, based on measurements recorded every 30 min. Data from previous years indicated that, while average summer water temperature was similar at the upstream (13.8°C) and downstream (14.0°C) ends of the study reach, diel fluctuations in water temperature were smaller upstream (means for August 1993: 1.8°C upstream and 4.8°C downstream).

We used 18 instream enclosures to measure habitat-specific survival and growth of two size-classes of juvenile steelhead. The enclosures were created by placing 6-mm mesh plastic screen across the stream perpendicular to the flow at the upstream and downstream ends of each section. Enclosed sections were 6-9 m in length and 14-21 m² in area at the beginning of the experiment. Over the course of the experiment, enclosed sections declined an average 8% in area and 18% in volume.

The 18 enclosures were categorized as either shallow or deep. The nine shallow habitats had maximum depths of 15-20 cm and average depths of 8-10 cm. The nine deep habitats had maximum depths of 42-50 cm and average depths of 20-24 cm. Low water velocities predominated in both kinds of habitats, although each experimental unit included approximately 1.5 m of riffle at the upstream end of the enclosed section. Riffles were generally <5 cm deep. We did not manipulate instream cover. Deep habitats all had substantial cover in the form of large woody debris and unembedded cobbles and boulders; cover was scarce in shallow habitat.

Although the enclosures prevented emigration by fish, steelhead emigration rates during summer are extremely low in Caspar Creek under natural conditions. Continuous downstream migrant trapping from June to October 1968 at a sampling site on the North Fork of Caspar Creek and a second site on a Caspar Creek tributary of similar size yielded only six steelhead, all age 0 (Burns 1972).

For the experiment, we utilized two size-classes of steelhead, which reflected the size-frequency distributions in the study area during August of previous years (R.J. Nakamoto, unpublished data).

These distributions had two peaks at approximately 50- and 100-mm fork length (FL), which we refer to as age-0 and age-1 fish. We compared interactions within versus between size-classes using three different combinations of the two size-classes: (i) age 0 alone, (ii) age 1 alone, and (iii) 50% age-0 fish and 50% age-1 fish (on the basis of biomass). Total steelhead biomass per area was the same in all treatments. The three size-class combinations were randomly assigned within the two sets of enclosures on the basis of habitat (nine shallow and nine deep), with three replicates per treatment combination.

We stocked steelhead in enclosures on the basis of an area-specific biomass derived from the mean biomass in June 1994, prior to the experiment. The mean was based on three electrofishing passes in 44 habitat units within the study reach representing the range of habitat types available. After manipulation, each enclosure contained a biomass of approximately 2.1 g·m⁻², which was 75% of the overall average biomass from the June sampling. We used a lower than natural density of steelhead because we anticipated loss of habitat over the course of the experiment as a result of declining discharge. We suspected that loss of habitat would negatively affect the growth and survival of steelhead, and we sought to avoid high mortality unrelated to the treatments. By using a fish density slightly lower than natural, we also hoped to minimize any effects of the enclosures by reducing the probability that fish would attempt to emigrate as density increased with declining habitat.

After erecting the fences, we removed all fish by making four to six electrofishing passes through the enclosures. We then added fish to each enclosure in the size and number appropriate for the size-class treatment and a total density of 2.1 g·m⁻² (overall mean for the 18 experimental units 2.1 ± 0.05 g·m⁻² (mean ± SE)). Individual fish were measured to the nearest 1 mm FL and weighed on an electronic balance to the nearest 0.01 g. Age-0 fish added to the enclosures were 45-63 mm FL and averaged 55 ± 0.3 mm ($n = 170$). Age-1 fish were 80-102 mm FL and averaged 91 ± 1.0 mm FL ($n = 40$). Treatments with only age-0 fish contained 13-22 fish. Treatments with only age 1 fish held four or five fish. Enclosures with equal biomasses of the two size-classes contained 8-10 age-0 and 2 or 3 age-1 fish. Fish were not marked individually, to avoid any short-term effects of marking on growth rates. Natural salamander densities were not altered.

At the end of the experiment, fish were removed from the enclosures by making four to six electrofishing passes, then counted, measured, and weighed so that survival and growth could be quantified. For age-0 fish, we estimated growth by determining the percent change in mean mass during the experiment. We used the same procedure for age-1 fish, except for two cases in which we compared the lengths of age-1 fish stocked and of those recovered, and determined the identity of missing fish by assuming that no fish in the enclosures lost >4 mm FL. For those observations, we measured the percent change in mass on the basis of the initial and final masses of the fish recovered at the end of the experiment.

We analyzed the effects of habitat, size-class, and their interaction on steelhead survival (each with 1 and 8 df) using analysis of variance (ANOVA). We separately analyzed results for age-0 and age-1 fish by comparing the treatments containing one size-class with the combined size-class treatment. Analyses of fish growth were the same with one exception. Because the gradient in diel fluctuation in water temperature within the study reach could have affected steelhead energetics (Hokanson et al. 1977; Duthie and Houlihan 1982; Vondracek et al. 1982a, 1982b; Henry and Houston 1984), we included the longitudinal position of the experimental units as a covariate in the analyses of fish growth.

Results

The survival of age-0 steelhead was not related to habitat or size-class treatment (all three P values from two-way ANOVA > 0.50; Table 1). Survival of age-0 steelhead ranged

Table 1. Percent survival (mean \pm SE) of two age-classes of juvenile steelhead in the presence or absence of the other age-class, in shallow and deep habitats, during a 6-week experiment in North Fork Caspar Creek, California, in summer 1994 ($n = 3$ for each treatment combination).

Treatment	Shallow		Deep	
	Age 0	Age 1	Age 0	Age 1
Age 0 only	80 \pm 10		81 \pm 10	
Age 1 only		74 \pm 4		92 \pm 8
Age 0 + age 1	80 \pm 20	89 \pm 11	73 \pm 3	89 \pm 11

from 70 to 100% in all enclosures, with the exception of the experimental unit that suffered the greatest loss in wetted area during the experiment (30% loss in area). The survival of age-0 fish was 40% in this unit, a shallow habitat that contained both size-classes. The overall survival of age-0 fish and gape limitations of age-1 fish suggest that cannibalism was not a factor in this experiment.

Mean mass change of age-0 fish in all treatment combinations was positive and also was unrelated to the treatments (analysis of covariance (ANCOVA); all $P > 0.50$; Fig. 1). Analysis of growth of age-0 fish with and without the covariate (the longitudinal position of the experimental units) yielded similar results (ANOVA; all $P > 0.50$).

Survival of age-1 steelhead was high and unrelated to treatments (all three P values from two-way ANOVA > 0.35 ; Table 1). Survival was 100% for age-1 fish in 6 of the 12 units they occupied, and one fish was not recovered from each of the other 6 units. While we suspect that the six age-1 fish that we did not recover were removed by predators, our sampling efficiency may have been $<100\%$ for both size-classes, resulting in underestimation of survival.

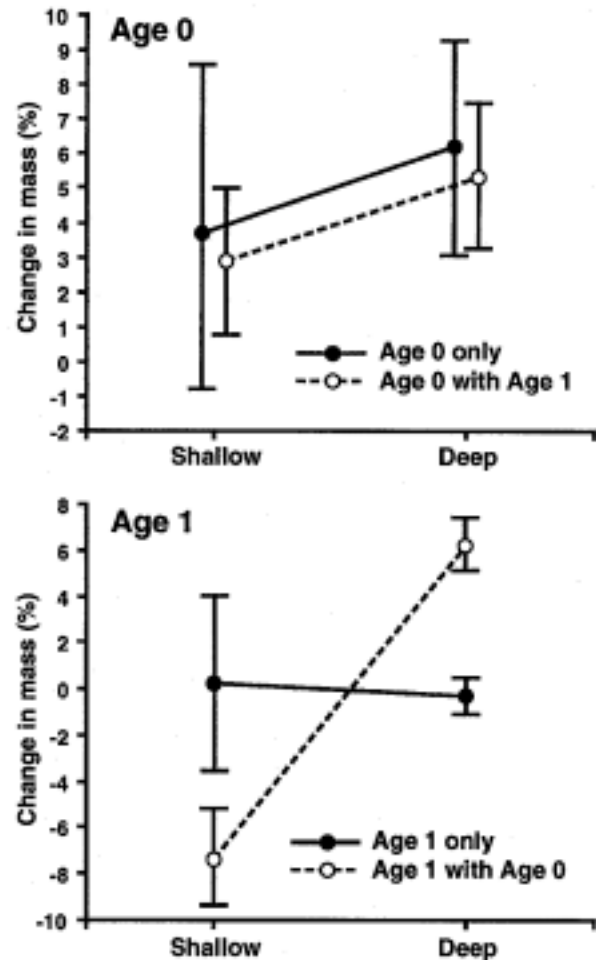
The growth of age-1 fish, however, varied significantly among treatments. Age-1 fish gained mass only in deep habitats containing both size-classes, and lost mass in shallow habitats containing both size-classes (Fig. 1). Mass change of age-1 steelhead in the absence of age-0 fish did not differ significantly from zero in shallow or deep habitats. Both the depth \times size-class interaction ($F_{[1,7]} = 12.15$, $P = 0.010$) and depth ($F_{[1,7]} = 10.55$, $P = 0.014$) were significant terms in the ANCOVA of age-1 growth. Exclusion of the covariate again produced similar results to those of ANCOVA (ANOVA; depth \times size-class interaction: $F_{[1,8]} = 11.49$, $P = 0.010$; depth: $F_{[1,8]} = 9.82$, $P = 0.015$).

Failure to recover all fish stocked within the enclosures appeared to have little effect on our estimates of fish growth. Within treatments, estimates of growth by age-1 fish were similar for replicates from which all age-1 fish stocked were recovered and those from which one age-1 fish was not recovered. For example, growth of age-1 fish with age-0 fish in deep habitats averaged 6% for all three replicates and 7% for the two replicates in which all age-1 fish were recovered. Similarly, mass loss of age-1 fish with age-0 fish in shallow habitats averaged -7% for all three replicates and -8% for the two replicates in which all age-1 fish were recovered.

Discussion

This experiment shows that relatively small differences in habitat and in fish size can have significant consequences for

Fig. 1. Mean change in mass of two age-classes of juvenile steelhead in the presence or absence of the other age-class, in shallow and deep habitats, during a 6-week experiment in North Fork Caspar Creek, California, in summer 1994 ($n = 3$ for each treatment combination). Points in the top graph are offset for clarity. Error bars are ± 1 SE.



intraspecific interactions among juvenile steelhead. The most striking result was that the mass change of large juvenile steelhead when they occupied enclosures with age-0 fish was dramatically different in shallow and deep habitats. In contrast, the growth of age-1 fish in single size-class treatments was unaffected by habitat, yet different from the mixed size-class treatments in both habitats. Several possible differences between the two types of habitat and between the two size-classes of steelhead used in the experiment deserve consideration when attempting to explain these results.

Shallow and deep habitats may have differed in the amount of food they provided to juvenile steelhead. The pattern of total mass gain by steelhead in shallow and deep habitats supports the suggestion that food availability was greater in deep habitats. While the higher average water velocity and slightly larger substrate in shallow habitats may have supported a more abundant benthic fauna, individual prey might have been more available to fish on the finer substrate in deep habitats. Gilliam et al. (1989) demonstrated the ability of creek chub (*Semotilus atromaculatus*) to reduce the abundance of invertebrates in

artificial stream channels with silt-mud substrate, while Power (1992) documented the failure of steelhead and California roach (*Hesperoleucus symmetricus*) to reduce the abundance of invertebrates inhabiting gravel substrate in a California river. Also, invertebrates drifting from shallow riffles upstream into the areas of our enclosures occupied by fish may have drifted further in the deeper enclosures (Allan and Feifarek 1989) and thus been more available to juvenile steelhead. Finally, steelhead, particularly age-1 fish, were probably able to forage in a smaller fraction of the shallow enclosures because of their inability to swim in extremely shallow water.

The biomass-specific metabolic rate of animals declines with increasing body size. Because we held biomass constant among treatments, the total maintenance requirements for all steelhead in the enclosures should have been highest in the treatments comprised only of age-0 fish and lowest where only age-1 fish were present. Using the relationship between body size and metabolic rate established for sockeye salmon (*Oncorhynchus nerka*) at 15°C by Brett and Glass (1973), we estimated the overall area-specific basal metabolic rate ($\text{mg O}_2 \text{ h}^{-1} \text{ m}^{-2}$) for steelhead in each enclosure at the beginning of the experiment by summing the individual estimated metabolic rates of each fish added. This analysis revealed that, as predicted, the overall metabolic rate for steelhead was highest in treatments with only age-0 fish and lowest in treatments with only age-1 fish, but the overall metabolic rates in treatments contrasted in our analysis (age 0 only vs. age 0 - age 1; age 1 only vs. age 0 - age 1) were not significantly different.

The difference in body size between the two age-classes also dictated that the total numbers of fish varied among treatments because biomass was held constant. For example, age-1 fish occupied the enclosures with either 3 or 4 conspecifics (treatments with only age-1 fish) or over 10 conspecifics (age-0 - age-1 treatments). The lower growth of age-1 fish enclosed with age-0 fish in shallow water compared with their growth in treatments with only age-1 fish supports the hypothesis that the total density of fish in an enclosure influenced growth rate. However, deep habitats yielded the opposite result for age-1 steelhead, and growth of age-0 fish was very similar between age-class treatments in both shallow and deep habitats.

The frequency of agonistic behavior probably differed between the two size-classes of steelhead and among treatments in the experiment. Ryer and Olla (1991) observed that aggressive behavior increased with body size in juvenile chum salmon (*Oncorhynchus keta*), while Chandler and Bjornn (1988) found that aggressive interactions in juvenile steelhead occur mainly between fish of similar size. Spatial segregation by body size is common among salmonids (e.g., Everest and Chapman 1972). These observations suggest that fish in treatments containing only age-1 steelhead expended more energy on agonistic interactions than fish in the other size-class treatments, at least within the same kind of habitat.

Differences between the two size-classes in predator avoidance behavior may also have contributed to our results. Grant and Noakes (1987) found a negative relationship between fish size and distance to cover in juvenile brook trout (*Salvelinus fontinalis*). Grant and Noakes also found that reactive distance to an approaching observer and time before returning to foraging following disturbance were positively related to fish size for age-0 brook trout. The positive relationship between fish size and predator avoidance behavior probably increases in

strength with decreasing habitat depth, considering the likely depth dependence of predation risk (Power 1987; Harvey and Stewart 1991). Under natural conditions and in the enclosures, age-0 steelhead in Caspar Creek often occupied microhabitats so shallow that their movement was detected easily by disturbance of the water's surface (B.C. Harvey and R.J. Nakamoto, personal observations). In contrast, age-1 fish in shallow enclosures were never apparent to streamside observers during the experiment, while age-1 fish in deep habitats were often visible. Greater predation risk can result in reduced growth rates in fishes (Tabor and Wurtsbaugh 1991; Fraser and Gilliam 1992).

The previous discussion suggests that the following mechanisms contributed to the strong differences among treatments for age-1 steelhead. Shallow habitats may have been inferior for age-1 steelhead because of (i) lower food availability and (ii) greater predator avoidance behavior by age-1 fish in shallow water. The single size-class treatment may have been superior to the mixed size-class treatment for age-1 fish in shallow water (i) because of the lower density of fish in the former treatment and (ii) because age-0 fish, which were not engaged in extensive predator avoidance behavior in shallow water, were more effective foragers in that habitat, reducing foraging opportunities for age-1 fish. Also for age-1 fish, the mixed size-class treatment may have been superior to the single size-class treatment in deep habitats because (i) reduced vigilance for predators compared with shallow habitats allowed age-1 fish to utilize their larger size in defending feeding positions in the mixed size-class treatment and (ii) reduced vigilance for predators increased the opportunity for agonistic interactions among age-1 fish, particularly in the treatment with only age-1 fish. The latter hypothesis is supported by the pattern of mass change in treatments with only age-1 fish: in all three replicates in deep habitats the variance in individual masses increased over the course of the experiment, while the variance in individual masses of age-1 steelhead declined in the three replicates in shallow habitats.

Our results suggest that competition between size-classes contributes to increases in the biomass of age-0 salmonids relative to older fish in small low-gradient streams where water depth and habitat complexity are reduced (Burns 1972; Bisson and Sedell 1984). The benefits of deep pool habitat for large juvenile salmonids in the presence of smaller fish are probably greatest in such streams, where alternative habitats are extremely shallow and surface turbulence rarely provides cover for fish. In Caspar Creek, the physical setting strongly influences interactions between size-classes of juvenile steelhead such that large fish are successful only in a subset of the available habitat. In some streams, competitive interactions may contribute to the bigger-deeper pattern of fish distribution (e.g., Power 1984; Harvey 1991), which has previously been attributed strictly to predation risk.

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