Transactions of the American Fisheries Society 125:237-243, 1996
American Fisheries Society 1996

Effects of Steelhead Density on Growth of Coho Salmon in a Small Coastal California Stream

BRET C. HARVEY AND RODNEY J. NAKAMOTO

Pacific *Southwest Research Station, U.S. Forest Service*
1700 Bayview Drive, Arcata, California 95521 USA

Abstract.-Weight change in age-0 coho salmon *Oncorhynchus kisutch* at about natural density was negatively related to the density of juvenile steelhead (anadromous rainbow trout *O. mykiss*) in a 6-week experiment conducted in July-August 1993 in the north and south forks of Caspar Creek, California. The experiment used 12 enclosed stream sections, each containing a pool and a portion of upstream riffle, with two replicates of three steelhead densities-zero, natural density (1X), and twice the natural density (2X)-on both the north and south forks. The natural density of coho salmon was about one-sixth the density of steelhead. Coho salmon survival was high (87% overall) and not related to treatments. In the north fork, coho salmon weight change was positive in zero density steelhead treatments, zero in 1X treatments, and negative in 2X treatments. Coho salmon weight change in the south fork was less favorable than in the north fork but was also negatively related to the density of steelhead. These results indicate that under some conditions resource partitioning by salmonid species does not eliminate negative interspecific interactions.

Interspecific interactions between salmonid species have received considerable attention from fisheries biologists, yet there are few well-documented field examples of negative interspecific effects on population size in the absence of substantial changes in habitat (Moore et al. 1983, 1986; Larson and Moore 1985). Also, few field studies have measured interspecific effects on parameters related directly to survival and reproduction, such as growth (Kennedy and Strange 1980, 1986a).

Much of the focus in research on salmonids has been on habitat partitioning (Hearn 1987). Many studies have provided evidence for microhabitat partitioning (e.g., Everest and Chapman 1972; Cunjak and Green 1983; Glova 1987; Dolloff and Reeves 1990), and some have documented habitat shifts following the removal of one species (e.g., Fausch and White 1981; Hearn and Kynard 1986; Kennedy and Strange 1986b; DeWald and Wilzbach 1992). However, even where habitat segregation leads to dietary differences between species (Johnson and Ringler 1980; Glova 1984), it may not obviate competition for food (Chapman 1966). Where segregation results from ongoing interactions, species that shift in response to the presence of another may then occupy habitats that provide lower net energy intake (although predation risk may confound habitat selection based on energetic considerations alone). Also, spatial separation of species on a microhabitat scale may not preclude significant overlap in the use of food resources, particularly where drifting prey are significant components in the diets of both species (Fausch and White 1986).

In situations where significant habitat segregation does not occur, competition between salmonid species should be more likely. Where differences in the densities of species are large, interspecific segregation of habitat could become weaker as intraspecific interactions dominate the interactions of the more abundant species. Some physical settings may provide limited opportunities for segregation by habitat. For example, habitat partitioning at the scale of channel geomorphic units (e.g., pools, riffles) may be restricted in small streams if fast-water habitats are too shallow to be occupied by fish. The simplification of stream channels by aggradation and the removal of wood debris may also reduce opportunities for habitat partitioning. Finally, smaller channel geomorphic units probably reduce the extent of microhabitat partitioning that is possible.

In many small California coastal streams, populations of coho salmon *Oncorhynchus kisutch* and steelhead (anadromous rainbow trout *O. mykiss*), and the habitat available, exemplify the conditions outlined above. As a result of widespread declines in coho salmon populations in California (Brown et al. 1994), many streams contain small numbers of coho salmon in sympatry with higher densities of steelhead. Most of these streams have been subject to anthropogenic habitat alterations. In light of this situation, and the paucity of data on the effect of interspecific interactions on salmonid growth, we tested the hypothesis that juvenile steelhead negatively affect coho salmon survival

and growth in two streams offering common habitat conditions for the two species in northern California. We focused on the effect of steelhead on coho salmon rather than attempting to contrast inter- and intraspecific competition because abundances of the two species in many streams suggest that, for coho salmon, interspecific interactions are currently of overriding importance.

Study Streams

Caspar Creek is a small coastal stream in Mendocino County, California. It originates at 245 m elevation and flows 13 km before emptying into the Pacific Ocean at 39°22'N 123°49'W We conducted this study in two reaches at similar longitudinal positions on the north and south forks. The downstream end of the north fork reach has a drainage area of about 497 ha, and that of the south fork about 424 ha. Both reaches have a 1-2% gradient. Both streams have measuring weirs within 150 m of the downstream ends of the study reaches. During the experiment, discharge declined steadily from 0.74 to 0.26 m^3/min in the north fork and from 0.65 to 0.25 m^3/min in the south fork. Water temperatures measured hourly during the experiment averaged 13.9°C in the north fork and 13.5°C in the south fork.

The two drainages have been used in watershed scale experiments on the effects of timber harvest practices. The entire south fork was selectively logged in 1971-1973. About 40% of the north fork was logged by clearcutting in 1989-1991; selectively cut buffer strips of 40 m were left throughout the study reach and upstream. Forest cover in both drainages includes 100-year-old second-growth coastal redwood *Sequoia sempervirens* and Douglas-fir *Pseudotsuga menziesii*. Tan oak *Lithocarpus densiflora,* huckleberry *Vaccinium ovatum,* and sword fern *Polystichium minutum* predominate in the understory. Alder *Alnus rubra* dominates the riparian zone of the south fork, but is absent from the north fork.

Coho salmon and steelhead were the only two fish species in the north fork study reach; the downstream end of the south fork study reach also contained a low density of threespine stickleback *Gasterosteus aculeatus.* Pacific giant salamanders *Dicamptodon tenebrosus* were abundant in both streams. During the experiment, all coho salmon in the two study reaches were age-0. Of the 1,375 steelhead sampled in both areas, about 95% were age-0. Examination of size distributions suggested an upper limit of 80 mm fork length (FL) for age-0 steelhead (R. J. Nakamoto, unpublished data).

Methods

We used a cross-classified experimental design to measure the effect of juvenile steelhead on age 0 coho salmon growth and survival within fenced stream sections in the north and south forks of Caspar Creek over 6 weeks, from 19 July to 31 August 1993. We included two streams in the de sign of the experiment because of consistent differences in their fish densities over the previous 5 years (Nakamoto, unpublished data). Coho salmon in the fenced stream sections were stocked at about natural density, and the steelhead treatments were zero density, natural density (1 X), and twice the natural density (2 X). The experiment included two replicates of each density treatment in each stream, allowing analysis of steelhead density, stream, and steelhead density X stream interaction effects on coho salmon survival and growth. We estimated natural coho salmon and steelhead densities before the experiment by blocknetting 24 pools in the north fork and electrofishing them to depletion (three to five passes with a backpack electroshocker).

Experimental units were positioned within the area naturally occupied by both species. Each experimental unit was a stream section of 13.5-19.6 m^2 containing a single lateral scour pool with a 2-m length of upstream riffle. Maximum water depths within units ranged between 45 and 60 cm. We constructed fences at the upstream and downstream ends of each experimental unit using 6-mm-mesh plastic screen. We assumed the mesh had little or no effect on food availability; invertebrates that could not pass through this screen were probably too large to have been eaten by fish used in the experiment. Experimental units were separated by an average of 85 m in the north fork and 106 m in the south fork. The three steelhead density treatments were randomly assigned to the six experimental units in each stream.

All 12 unmanipulated pools contained some cover for fish, but we also added a 92 X 71-cm wood panel to each pool to provide a substantial refuge in each experimental unit. Each panel was completely submerged near the middle of the pool with the long axis of the panel parallel to the flow. One long edge of the panel was anchored to the substrate with rocks and the opposite edge positioned about 20 cm off the bottom.

At the beginning of the experiment, we first electrofished each unit (four or five passes) to remove all fish, which were retained in buckets. Pacific giant salamanders were also captured during

electrofishing; those that we considered large enough to be piscivorous were removed from the enclosures. We then added the appropriate numbers of coho salmon and steelhead, based on earlier determination of the natural densities of both species, measurement of the areas of the experimental units, and assignment of steelhead density treatments to specific units. We measured all fish stocked into the units to the nearest millimeter (FL) and individually weighed them to the nearest 0.01 g with an Ohaus model CT200 electronic balance. Fish stocked into a given unit were an uncontrolled mixture of fish previously removed from that unit and fish captured elsewhere in the study reach. We attempted to approximate the natural size-frequency distribution of steelhead when stocking the 1X and 2X treatments. Thus, steelhead treatments contained a small number of steelhead longer than 80mm FL and shorter than 55 mm FL. The size of coho salmon used in the experiment also reflected the natural size-frequency distribution; they ranged from 59 to 72 mm FL. Individual fish were not marked or tagged to avoid possible effects on short-term growth. We cleaned enclosure fences every 6-8 d. Only small quantities of detritus accumulated on the fences between cleanings. At the end of the experiment, all fish in the experimental units were collected by electrofishing and again individually measured and weighed.

The 1 X treatment represented natural density of age-0 steelhead in north fork pools (1.5 fish/m^2); 22-28 steelhead were added to enclosures receiving the 1X treatment. Enclosures containing the 2X treatment received 41-50 steelhead. All enclosures received 5-6 coho salmon, which represented about 0.3 coho salmon/m2. This density was higher than the natural density of 0.2 fish/m^2 that we measured in the north fork. However, historic densities of coho salmon in Caspar Creek have exceeded the density we used in the experiment. In summer 1969, coho salmon density in an entire reach of the north fork was 0.6 fish/m^2 (Burns 1971), and in summer 1990, coho salmon density in south fork pools was 0.4/m2 (Nakamoto, unpublished data).

We used two-way analysis of variance (ANOVA; main effects: stream and steelhead density) to analyze survival and growth of coho salmon. Survival data were transformed before ANOVA by means of the arcsine square root transformation as modified by Anscombe (1948) for binomial data. Growth of coho salmon was expressed as percent change from initial weight. Where all the coho salmon stocked in an enclosure were not recovered, we estimated weight change based on the average weight of individuals at the beginning and end of the experiment. We also analyzed steelhead survival by two-way ANOVA using transformed data from the 1X and 2X treatments. Response variables were tested for homogeneity of variance with Bartlett's test.

Results

The integrity of all enclosure fences was maintained throughout the experiment. However, all of the zero density steelhead treatments contained three to six small (<50 mm FL) steelhead at the end of the experiment. Either we failed to remove these fish from the enclosures at the beginning of the experiment or they passed through the fences. The first possibility is supported by our recovery of individuals shorter than 50 mm FL (both living and dead) from all treatment combinations. In either case, these fish represented a very small fraction of the biomass of fish in any treatment, and were probably evenly distributed among treatments.

Coho salmon exhibited high survival in the experiment (87% overall). We recovered all of the coho salmon stocked in 7 of the 12 experimental units (Table 1). Survival was not related to treatments ($P \geq 0.238$ for both main effects and the interaction term).

Growth of coho salmon varied among the treatments. Steelhead negatively affected coho salmon growth (Figure 1), and steelhead density was the dominant factor in the analysis of variance (F = 49.3; df = 2, 5; $P < 0.001$). All three pairwise comparisons of coho salmon growth among the three steelhead density treatments were signifycantly different (Dunn-Siddk test, $P < 0.05$). In the north fork, coho salmon gained weight in the zero density steelhead treatment, did not change weight in the 1 X treatment, and lost weight in the 2X treatment (Figure 1). Coho salmon growth was lower in the south fork than in the north fork (F = 8.8; df = 1, 5; P = 0.031). The steelhead density X stream interaction term was not significant (F = 4.3; df = 2, 5; P = 0.083). The ANOVA of coho salmon growth contained 5 degrees of freedom for error and 10 degrees of freedom total because we excluded from the analysis the enclosure from which we recovered only two coho salmon, and therefore included a total of 11 observations. We did so because the two surviving fish in that enclosure seemed to have been the two smallest of the five fish stocked, based on the length of fish

TABLE 1.-Survival and size change of coho salmon in enclosures with varying steelhead density in the north and south forks of Caspar Creek, 19 July-31 August 1993. The two replicates of each steelhead density treatment in each stream are represented as R1 and R2. Steelhead densities are zero (0), natural density of steelbead in the north fork of Caspar Creek (1X), and twice the natural density (2X).

Location and variable	Steelhead density: 0		1X		2X	
	R1	R2	R1	R2	R1	R2
North fork						
Number stocked	5	5	5	5	5	5
Number recovered	5	5	3	4	5	5
Initial length (mm)	62-75	63-67	64-67	63-71	61-70	62-73
Final length (mm)	68-82	67-70	66-69	65-71	62-74	67-74
Initial mean weight (g)	4.07	3.19	3.44	3.55	3.56	4.21
Final mean weight (g)	4.72	3.69	3.49	3.55	3.31	3.93
South fork						
Number stocked	6	5	6	5	5	5
Number recovered	5	5	5	5	5	2
Initial length (mm)	60-72	60-68	59-72	59-68	59-69	62-69
Final length (mm)	64-73	63-72	62-73	61-70	60-67	62-64
Initial mean weight (g)	3.99	3.34	3.49	3.25	3.35	3.58
Final mean weight (g)	4.17	3.52	3.37	3.07	3.03	2.83

stocked and recovered. Thus, the estimate of coho salmon growth in that enclosure was biased. Assuming that we recovered the two smallest fish stocked in that enclosure, their weight loss was 6.8%, similar to the result for the replicate enclosure of the 2X treatment in the south fork in which all coho survived (9.3% weight loss). Errors in the estimation of growth in the other four enclosures from which some coho salmon were not recovered contributed to experimental error, providing a more conservative test of treatment effects.

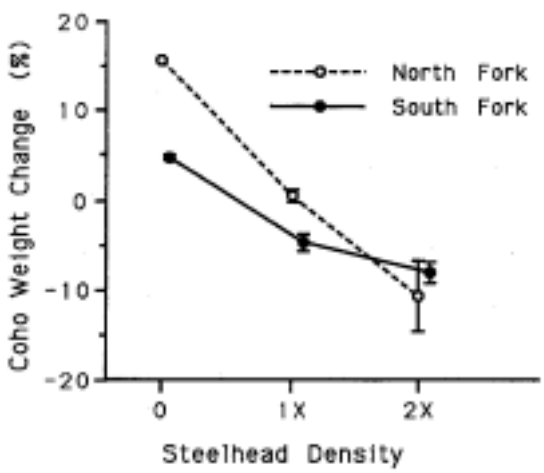

FIGURE 1.- Growth of coho salmon in experimental enclosures in Caspar Creek, 19 July-31 August 1993. Growth is expressed as the change in average size of individuals in each treatment. The exception was one observation with less than 100% survival in which surviving individuals could be identified based on the assumption that fish did not lose more than 3 mm FL during the experiment. Points are means of two replicates; vertical lines are ±SE (standard errors for growth of coho salmon at zero steelhead density fit within the data points). Points representing the two streams at each steelhead density are offset so that SEs can be observed.

Steelhead survival was lower in the 2X treatments than in natural density treatments (F = 7.76; df = 1, 4; P < 0.050; Table 2). Our observations of dead fish in the enclosures suggested that mortality in the 2X treatments was consistent over the course of the experiment. Steelhead survival did not differ significantly between streams (F = 2.60; df = 1, 4; P = 0.182), and the interaction between

TABLE 2.-Stocking and recovery of steelhead in enclosures with varying steelhead density in the north and south forks of Caspar Creek, 19 July-31 August 1993. The two replicates of each steelhead density treatment in each stream are represented as R1 and R2; X is the natural density of steelhead in the north fork of Caspar Creek.

Location and variable	Steelhead density: 1X		2X	
	R1	R2	R1	R2
North fork				
Number stocked	24	25	41	50
Percent recovered	72	100	64	78
South fork				
Number stocked	22	28	47	49
Percent recovered	82	86	35	47

steelhead density and stream was also not significant (F = 0.86; df = 1, 4; P = 0.407), although these tests have low statistical power. Steelhead survival seemed particularly low in the south fork 2X treatment (Table 2).

Discussion

The presence of juvenile steelhead had a clear, negative effect on the growth of age-0 coho salmon in our experiment. Reduced growth is likely to have population level consequences for coho salmon because juvenile size is related to the probability of survival and reproduction in salmonids (Bilton et al. 1982; Ward and Slaney 1988). Our result parallels the observation that age-0 Atlantic salmon *Salmo salar* in a reach of stream that also contained brown trout *Salmo trutta* grew more slowly than those in a reach without brown trout (Kennedy and Strange 1980, 1986a). Our experiment did not include the treatments necessary to compare intra- and interspecific competition in coho salmon and steelhead in Caspar Creek, in part because both pools and coho salmon were rare.

The differences we observed in coho salmon growth between the two forks of Caspar Creek may reflect natural differences in resource availability. The biomass of juvenile salmonids has averaged 40% greater in the north fork than in the south fork over a 5-year period, based on 383 density measurements in specific habitat units (Nakamoto, unpublished data). Absence of weight change by coho salmon in the north fork 1 X treatment, which provided nearly natural densities of both species, suggests a strong link between natural density and available resources. Hanson and Leggett (1985) obtained the same result from an enclosure experiment with yellow perch *Perca flavescens* and bluegill *Lepomis macrochirus* in the littoral zone of a lake: no growth during summer by fish at natural density in the absence of substantial mortality. Relatively low resource availability in the south fork may explain the particularly low survival of steelhead in the south fork 2X treatment. This treatment probably represented the greatest disparity between salmonid density and available resources, and the fences prevented reduction in density by emigration.

Interestingly, both this study and those of Kennedy and Strange (1980, 1986a) involved species with an evolutionary history of sympatry. Stronger interspecific interactions might be predicted for salmonid species that have not coevolved because such taxa may overlap more strongly than coevolved species in their use of resources (Fausch and White 1986; Fausch 1988). In fact, there are numerous observations of differences between sympatric steelhead and coho salmon in the use of habitat at both the channel geomorphic unit (Hartman 1965; Bisson et al. 1988) and microhabitat scales (Sheppard and Johnson 1985; Bugert et al. 1991; Bugert and Bjornn 1991). In addition, Johnson and Ringler (1980) observed differences in the diets of sympatric coho salmon and steelhead. Both habitat and diet partitioning between the two species are also evident in Caspar Creek. Similar to the pattern observed by Bugert et al. (1991), coho salmon are most often observed near the middle of Caspar Creek pools, while steelhead are more broadly distributed (B. C. Harvey, personal observations). Coho salmon in Caspar Creek also seem to include a higher proportion of terrestrial invertebrates in their diet than do steelhead (David Fuller, U.S. Bureau of Land Management, personal communication).

For several reasons, resource partitioning may not eliminate the negative effect of a natural density of steelhead on coho salmon in Caspar Creek. First, partitioning of habitat and food resources at the scale of channel geomorphic units by coho salmon and steelhead (Johnson and Ringler 1980) is largely impossible in Caspar Creek, where most steelhead occupy pools because riffles are extremely shallow. Second, the pool habitat preferred by coho salmon is not a large proportion of the available habitat in Caspar Creek, and pools are small. Similar to other streams in logged drainages (Bilby and Ward 1991; Reeves et al. 1993), Caspar Creek has a relatively small quantity of large woody debris in the channel (O'Connor and Ziemer 1989). Several authors have found a positive relationship between the presence of large woody debris and pool frequency, volume, or depth (e.g., Bilby and Ward 1991; Fausch and Northcote 1992; Reeves et al. 1993; Ralph et al. 1994). Third, the use of microhabitat by coho salmon under natural conditions in Caspar Creek may reflect ongoing competition. In our zero-density steelhead treatments, coho salmon were consistently observed in more upstream positions within pools than those they had occupied in the same pools in the presence of steelhead. Considering the influence of body size on interactions among salmonids (e.g., Fausch and White 1986), the presence of a small number of steelhead larger than age-0 coho salmon may be the key to this pattern. To the extent that coho salmon rely on prey in the drift, their more downstream positions in the presence of steelhead will probably result in lower growth. Nielsen

(1992) observed faster growth and greater use of aquatic insects by coho salmon that defended territories at locations in a Washington stream where water velocity exceeded 0.06 m/s than by fish occupying areas with lower water velocity. Fourth, a variety of factors other than competition among juveniles (e.g., human harvesting and annual variation in the accessibility of the upper reaches of Caspar Creek to anadromous fish) contribute to the current densities of the two species.

Reeves et a1. (1993) found that salmonid species diversity is positively related to habitat complexity in Oregon streams. This study's result that interspecific interactions had effects on the growth of individuals, in combination with observations suggesting that the outcome of interspecific interactions in salmonids is highly dependent on the physical environment (e.g., Cunjak and Green 1984; Glova 1986; Fausch 1988, 1989), support the hypothesis that interspecific interactions are important in producing the pattern observed by Reeves et al. (1993). Under conditions that differ from those in our experiment, coho salmon may not be strongly affected by the presence of steelhead. For example, the presence of steelhead did not prevent an increase in coho salmon following enhancement of large woody debris and pool habitat in an Oregon stream (Crispin et al. 1993). Clearly, both local habitat features and density-influencing factors operating at larger spatial scales will affect the significance of interspecific interactions between salmonids.

Acknowledgments

We thank L. Brown, B. Goldowitz, T. Lisle, and G. Reeves for reviewing previous versions of this paper, and J. Bednar for field assistance. The California Department of Forestry provided access to Caspar Creek.

References

Anscombe, F J. 1948. The transformation of Poisson, binomial and negative-binomial data. Biometrika 35:246-254.

Bilby, R. E., and J. V. Ward. 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut, and second-growth forests in southwestern Washington. Canadian Journal of Fisheries and Aquatic Sciences 48:2499-2508.

Bilton, H. T., D. F Alderdice, and J. T. Schnute. 1982. Influence of time and size at release of juvenile coho salmon *(Oncorhynchus kisutch)* on returns at maturity. Canadian Journal of Fisheries and Aquatic Sciences 39:426-447.

Bisson, P A., K. Sullivan, and J. L. Nielsen. 1988. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. Transactions of the American Fisheries Society 117:262-273.

Brown, L. R., P B. Moyle, and R. M. Yoshiyama. 1994. Historical decline and current status of coho salmon in California. North American Journal of Fisheries Management 14:237-261.

Bugert, R. M., and T. C. Bjornn. 1991. Habitat use by steelhead and coho salmon and their responses to predators and cover in a laboratory stream. Transactions of the American Fisheries Society 120:486-493.

Bugert, R. M., T. C. Bjornn, and W. R. Meehan. 1991. Summer habitat use by young salmonids and their responses to cover and predators in a small southeast Alaska stream. Transactions of the American Fisheries Society 120:474-485.

Burns, J. W. 1971. The carrying capacity for juvenile salmonids in some northern California streams. California Fish and Game 57:44-57.

Chapman, D. W. 1966. Food and space as regulators of salmonid populations in streams. American Naturalist 100:345-357.

Crispin, V., R. House, and D. Roberts. 1993. Changes in instream habitat, large woody debris, and salmon habitat after the restructuring of a coastal Oregon stream. North American Journal of Fisheries Management 13:96-102.

Cunjak, R. A., and J. M. Green. 1983. Habitat utilization by brook char *(Salvelinus fontinalis)* and rainbow trout *(Salmo gairdneri)* in Newfoundland streams. Canadian Journal of Zoology 61:1214-1219.

Cunjak, R. A., and J. M. Green. 1984. Species dominance by brook trout and rainbow trout in a simulated stream environment. Transactions of the American Fisheries Society 113:737-743.

DeWald, L., and M. A. Wilzbach. 1992. Interactions between native brook trout and hatchery brown trout: effects on habitat use, feeding, and growth. Transactions of the American Fisheries Society 121: 287-297.

Dolloff, C. A., and G. H. Reeves. 1990. Microhabitat partitioning among stream-dwelling juvenile coho salmon, *Oncorhynchus kisutch,* and Dolly Varden, *Salvelinus malma.* Canadian Journal of Fisheries and Aquatic Sciences 47:2297-2306.

Everest, E H., and D. W. Chapman. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. Journal of the Fisheries Research Board of Canada 29:91-100.

Fausch, K. D. 1988. Tests of competition between native and introduced salmonids in streams: what have we learned? Canadian Journal of Fisheries and Aquatic Sciences 45:2238-2246.

Fausch, K. D. 1989. Do gradient and temperature affect distributions of, and interactions between, brook charr (Salvelinus fontinalis) and - other resident salmonids in streams? Pages 303-322 in H. Kawanabe, F Yamazaki, and D. L. G. Noakes, editors.

Biology of charrs and masu salmon. Physiology and Ecology Japan, Kyoto University, Kyoto, Japan.

Fausch, K. D., and T G. Northcote. 1992. Large woody debris and salmonid habitat in a small coastal British Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences 49:682-693.

Fausch, K. D., and R. J. White. 1981. Competition between brook trout *(Salvelinus fontinalis)* and brown trout *(Salmo trutta)* for positions in a Michigan stream. Canadian Journal of Fisheries and Aquatic Sciences 38:1220-1227.

Fausch, K. D., and R. J. White. 1986. Competition among juveniles of coho salmon, brook trout, and brown trout in a laboratory stream, and implications for Great Lakes tributaries. Transactions of the American Fisheries Society 115:363-381.

Glova, G. J. 1984. Management implications of the distribution and diet of sympatric populations of juvenile coho salmon and coastal cutthroat trout in small streams in British Columbia, Canada. Progressive Fish Culturist 46:269-277.

Glova, G. J. 1986. Interactions of food and space between experimental populations of juvenile coho salmon *(Oncorhynchus kisutch)* and coastal cutthroat trout *(Salmo clarki)* in a laboratory stream. Hydrobiologia 132:155-168.

Glova, G. J. 1987. Comparison of allopatric cutthroat trout stocks with those sympatric with coho salmon and sculpins in small streams. Environmental Biology of Fishes 20:275-284.

Hanson, J. M., and W. C. Leggett. 1985. Experimental and field evidence for inter- and intraspecific competition in two freshwater fishes. Canadian Journal of Fisheries and Aquatic Sciences 42:280-286.

Hartman, G. E 1965. The role of behavior in the ecology and interaction of underyearling coho salmon *(Oncorhynchus kisutch)* and steelhead trout *(Salmo gairdneri).* Journal of the Fisheries Research Board of Canada 22:1035-1081.

Hearn, W. E. 1987. Interspecific competition and habitat segregation among stream-dwelling trout and salmon: a review. Fisheries 12(5):24-31.

Hearn, W. E., and B. E. Kynard. 1986. Habitat utilization and behavioral interaction of juvenile Atlantic salmon *(Salmo salar)* and rainbow trout (S. *gairdneri)* in tributaries of the White River of Vermont. Canadian Journal of Fisheries and Aquatic Sciences 43:1988-1998.

Johnson, J. H., and N. H. Ringler. 1980. Diets of juvenile coho salmon *(Oncorhynchus kisutch)* and steelhead trout *(Salmo gairdneri)* relative to prey availability. Canadian Journal of Zoology 58:553-558.

Kennedy, G. J. A., and C. D. Strange. 1980. Population changes after two years of salmon *(Salmo salar* L.) stocking in upland trout *(Salmo trutta* L.) streams. Journal of Fish Biology 17:577-586.

Kennedy, G. J. A., and C. D. Strange. 1986a. The effects of intra- and inter-specific competition on the survival and growth of stocked juvenile Atlantic salmon, *Salmo salar* L., and resident trout, *Salmo trutta* L., in an upland stream. Journal of Fish Biology 28: 479-489.

Kennedy, G. J. A., and C. D. Strange. 1986b. The effects of intra- and inter-specific competition on the distribution of stocked juvenile Atlantic salmon, *Salmo salar* L., in relation to depth and gradient in an upland trout, *Salmo trutta* L., stream. Journal of Fish Biology 29:199-214.

Larson, G. L., and S. E. Moore. 1985. Encroachment of exotic rainbow trout into stream populations of native brook trout in the southern Appalachian Mountains. Transactions of the American Fisheries Society 114:195-203.

Moore, S. E., G. L. Larson, and B. Ridley. 1986. Population control of exotic rainbow trout in streams of a natural area park. Environmental Management 10:215-219.

Moore, S. E., B. Ridley, and G. L. Larson. 1983. Standing crops of brook trout concurrent with removal of rainbow trout from selected streams in Great Smoky Mountains National Park. North American Journal of Fisheries Management 3:72-80.

Nielsen, J. L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. Transactions of the American Fisheries Society 121: 617-634.

O'Connor, M. D., and R. R. Ziemer. 1989. Coarse woody debris ecology in a second-growth *Sequoia sempervirens* forest stream. U.S. Forest Service General Technical Report PSW-110.

Ralph, S. C., G. C. Poole, L. L. Conquest, and R. J. Naiman. 1994. Stream channel morphology and woody debris in logged and unlogged basins of. western Washington. Canadian Journal of Fisheries and Aquatic Sciences 51:37-51.

Reeves, G. H., E H. Everest, and J. R. Sedell. 1993. Diversity of juvenile anadromous salmonid assemblages in coastal Oregon basins with different levels of timber harvest. Transactions of the American Fisheries Society 122:309-317.

Sheppard, J. D., and J. H. Johnson. 1985. Probability-of-use for depth, velocity, and substrate by subyearling coho salmon and steelhead in Lake Ontario tributary streams. North American Journal of Fisheries Management 5:277-282.

Ward, B. R., and P A. Slaney. 1988. Life-history and smolt-to-adult survival of Keough River steelhead trout (Salmo *gairdneri)* and the relationship to smolt size. Canadian Journal of Fisheries and Aquatic Sciences 45:1110-1122.

Received October 24, 1994
Accepted August 10, 1995