

Temperature-Dependent Interactions between Juvenile Steelhead and Sacramento Pikeminnow in Laboratory Streams

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Abstract.—We examined the temperature dependence of interactions between juvenile steelhead *Oncorhynchus mykiss* and juvenile Sacramento pikeminnow *Ptychocheilus grandis* in laboratory streams. Growth of dominant steelhead in water 20–23°C was reduced by more than 50% in trials with Sacramento pikeminnow compared with trials with steelhead alone. Comparison of the two-species treatment with one with an equal density of fish comprised of steelhead alone indicated that the per capita effect of Sacramento pikeminnow was similar to the intraspecific effect of steelhead in water 20–23°C. In contrast, the growth of dominant steelhead in water 15–18°C was unaffected by Sacramento pikeminnow. The temperature-dependence of the effect of Sacramento pikeminnow on dominant steelhead was also reflected in the size of the area defended by steelhead and in the behavior of Sacramento pikeminnow under the two thermal regimes. Compared with all other treatment combinations, dominant steelhead defended the smallest areas when accompanied by Sacramento pikeminnow in warm water. Behavioral interactions with steelhead initiated by Sacramento pikeminnow were about 50 times more frequent in warm water. For the growth of subdominant steelhead, the effect of intraspecific competition exceeded the interspecific effect of Sacramento pikeminnow regardless of water temperature. While thermal regime affects the distributions of these two species, this experiment suggests that it also affects the outcome of competition between them.

Habitat alteration and exotic species are common challenges to the viability of native freshwater fishes (e.g., Moyle and Williams 1990). In many instances, these two factors can interact to affect native taxa. Although habitat alterations may allow establishment of introduced species in some systems (Moyle and Light 1996a, 1996b) or enhance the population sizes of introduced species in others, such changes may also enhance the per capita negative effects of introduced species on native taxa. For example, habitat alterations leading to increases in water temperature may expand the range or population size of introduced warm-water fishes and also increase their predation rates or competitive effects on native species with preferences for cool water. The effects of higher temperature on energetics and, thus, on predation rates are fairly clear (e.g., Hartman and Brandt 1995), and several studies illustrate that competitive interactions among fishes also can be sensitive to temperature (Baltz et al. 1982; Cunjak and Green

1986; Reeves et al. 1987; De Staso and Rahel 1994; Taniguchi et al. 1998).

Like many drainages worldwide, the Eel River in northwestern California has experienced habitat alterations, species introductions, and declines in native fish populations. Over the last 60 years, reductions in riparian vegetation along many streams have caused increases in maximum stream temperatures. At least 16 fish species have been introduced in the drainage, and 8 of these have established stable populations (Brown and Moyle 1997). Since the 1940s, populations of native species, including steelhead *Oncorhynchus mykiss*, chinook salmon *O. tshawytscha*, coho salmon *O. kisutch*, and anadromous cutthroat trout *O. clarki clarki*, have declined considerably, whereas pink salmon *O. gorbuscha* and chum salmon *O. keta* are probably extinct in the Eel River (Brown and Moyle 1997). At least 10 of the 14 native fishes are extinct, rare, or in decline (Brown and Moyle 1997).

One of the most abundant introduced species in the Eel River is the Sacramento pikeminnow *Ptychocheilus grandis*, a large cyprinid native to the nearby Sacramento–San Joaquin drainage. The species appears well adapted to conditions in the Eel River; it has dispersed throughout most of the drainage since its introduction around 1979

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(Brown and Moyle 1997). Studies of biotic interactions involving Sacramento pikeminnow have focused on predation. For example, an experiment by White and Harvey (2001) suggested that Sacramento pikeminnow have significantly increased predation risk for native sculpins *Cottus* spp. in the Eel drainage. Brown and Moyle (1991) and Brown and Brasher (1995) observed changes in the use of habitat by several Eel River fishes in the presence of large Sacramento pikeminnow, which the authors attributed to the threat of predation by Sacramento pikeminnow. Predation by northern pikeminnow *P. oregonensis* has been studied extensively in the Columbia River system (e.g., Knutsen and Ward 1999; Zimmerman 1999; Zimmerman and Ward 1999), and estimates of predation by northern pikeminnow on salmonids in that system motivated a large-scale pikeminnow control program (Beamesderfer et al. 1996).

In contrast to predation by pikeminnow, interspecific competition involving pikeminnow is largely unstudied. However, patterns of resource use by Sacramento pikeminnow and other stream fishes, including native fishes in the Eel River, reveal the potential for competition. For example, invertebrates predominate the diets of both juvenile steelhead and juvenile Sacramento pikeminnow. Although Sacramento pikeminnow tolerate higher water temperatures than steelhead (Cech et al. 1990), juveniles of the two species commonly co-occur in many systems, including tributaries of the Eel River (Harvey et al. 2002). However, if juvenile steelhead and Sacramento pikeminnow compete, the outcome may be strongly influenced by temperature, as it is for competition between steelhead and another cyprinid, the redside shiner *Richardsonius balteatus* (Reeves et al. 1987). In this paper we describe a laboratory experiment designed to measure the effects of juvenile Sacramento pikeminnow on the growth and stream position of juvenile steelhead with treatments that allow measurement of the temperature dependence of this interaction.

Methods

The experiment was conducted in two laboratory streams (Reeves et al. 1983), both divided into two experimental units about 5.6 m long and 0.8 m wide. Each of the four experimental units contained a riffle-pool-riffle sequence. Mean depth was 60 cm in pools and 35 cm in riffles. Cobbles overlaid about 70% of the stream bottom, which had a base layer of sand and gravel. Paddlewheels in each stream generated velocities of

5–15 cm/s. A timer controlled photoperiod, providing 15-h days and 9-h nights. Light levels changed over 30 min in morning and evening. Plexiglas interior walls allowed observation of fish.

The experiment included two water temperature regimes cross-classified with three different fish treatments. Two controlled water temperature treatments were selected to reflect the summer range of thermal regimes in most tributaries of the Eel River where steelhead are found (Harvey et al. 2002): daily ranges of 15–18°C (cool) and 20–23°C (warm). The minimum temperature occurred at 0700 hours and the maximum at 1700 hours. The fish treatments contained age-1 steelhead (75–100 mm fork length [FL]) or a combination of age-1 steelhead and age-1 Sacramento pikeminnow (also 75–100 mm FL). The fish treatments included (1) eight steelhead equaling a density of 1.8 fish/m², which is the upper end of the range of juvenile steelhead densities observed in Eel River tributaries (high-density steelhead treatment); (2) four steelhead (low-density steelhead treatment); and (3) four steelhead and four Sacramento pikeminnow (two-species treatment). Because individuals of the two species were very similar in size, patterns of biomass in the three treatments paralleled the patterns in numerical density.

We estimated the effect of interspecific competition with Sacramento pikeminnow on steelhead by contrasting the low-density steelhead and two-species treatments. We compared the effects of intraspecific and interspecific competition on steelhead by contrasting the high-density steelhead and two-species treatments. Trials, each lasting 14 d, were conducted in May, June, and July of 1996, making a total of 12 trials (3 periods × 4 experimental units) or two replicates of the six treatments (three fish treatments under two thermal regimes). In May the cool- and warm-temperature streams each received the high-density steelhead and two-species treatments (1 treatment/unit). In June the cool- and warm-temperature streams each received the low-density steelhead and two-species treatments, and in July the cool- and warm-temperature streams each received the low-density and high-density steelhead treatments.

Growth, survival, and stream position were measured in all 12 trials, and aggressive behavior was measured in 8 of the 12 trials. Growth was expressed as percent change in weight over each trial. Stream position was measured as the mean distance of fish from the upstream end of the experimental unit. Because fish took 1–2 d to estab-

fish territories, mean stream position was computed from three observations per day on days 3–14 of each trial. For growth, survival, and stream position, the responses of dominant and subordinate steelhead were analyzed separately. In 11 trials, a single dominant steelhead defended the most upstream feeding position in the experimental units and behaved more aggressively than subordinate individuals. Mean values for growth and stream position provided the data from each replicate for the analyses of subordinate steelhead.

Behavioral interactions were quantified in the last eight trials, including two low-density steelhead trials at each temperature, one high-density steelhead trial at each temperature, and one two-species trial at each temperature. Behavioral observations were usually made for 15 min three times per day, beginning on day 3 of the trials or 31–34 times per trial (total of 7.75–8.50 h of observation). To facilitate observations, only one-third of an experimental unit was examined during each observation period. All interactions among fish in a randomly selected third of an experimental unit were recorded during each observation period. Although the observer was visible to fish in the experimental units, data were recorded only for fish that appeared undisturbed.

We captured fish used in the experiment from tributaries of the Eel River by electrofishing, then held them in laboratory tanks in Arcata, California, for 16–20 d before transport in aerated tanks to the artificial streams at the U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station in Corvallis, Oregon. The holding period served to acclimate fish to the water temperatures used in the experiment and to accustom them to feeding on frozen brine shrimp. Temperature change during acclimation did not exceed 8°C. After being transported to Corvallis, fish were held in mesh enclosures in the artificial streams for 20–24 h to acclimate them to laboratory stream water. This entire procedure was followed for each of the three trial periods.

To begin the experiment, each fish was weighed to the nearest 0.01 g with an electronic balance and its fork length was measured to the nearest millimeter. To determine weight change and map the locations of individual fish, each fish was uniquely marked with a pan jet marker on the caudal fin, anal fin, or dorsal fin. Fish were fed frozen brine shrimp that entered the stream through holes in a polyvinyl chloride pipe placed along the substrate in the upstream 3 m of each experimental unit. Stream water pumped into a headbox melted

a 450 mL block of ice containing the shrimp and forced them into the feeder pipe over about 30 min. Most brine shrimp entered the stream through holes in the first 1 m of the pipe (similar apparatus described in Reeves 1988). All treatments received the same daily ration, equivalent to about 15% of the biomass in the high-density steelhead or two-species treatments. One-third of the daily ration was given in the morning, one-third at midday, and one-third in the evening. At the end of each trial, all surviving fish were collected and weighed.

Because all dominant steelhead survived, the growth of dominant steelhead was analyzed with analysis of variance (ANOVA) using temperature and fish combination as cross-classified factors. We separately analyzed the two preplanned contrasts: low-density steelhead versus two-species treatments and high-density steelhead versus two-species treatments. For subordinate steelhead, mean growth and survival were both included in a multivariate ANOVA (MANOVA) using the same factors and contrasts. Percent survival over the 14-d trial periods was arcsine-square-root-transformed before analysis to reduce heterogeneous variances. Dead fish were excluded from estimates of growth. Cochran's test indicated that untransformed growth data for both dominant and subordinate steelhead did not violate the assumption of homogeneity of variance. We also analyzed mean stream position for dominant and subordinate steelhead using ANOVA and the same approach as that used to analyze growth. Data on stream position did not violate the assumption of homogeneity of variances. Finally, for Sacramento pikeminnow we compared mean growth and survival together in cool versus warm two-species trials using a MANOVA. The mean position of Sacramento pikeminnow in cool and warm two-species trials was contrasted with a *t*-test.

Results

Contrast of the two-species and low-density steelhead treatments revealed temperature-dependent interspecific effects of Sacramento pikeminnow on dominant steelhead. In cool water, dominant steelhead grew similarly in the low-density steelhead and two-species treatments. In warm water, growth of dominant steelhead in the low-density steelhead treatment averaged more than two times the growth of dominant steelhead in the two-species treatment (Figure 1; ANOVA of fish treatment \times temperature interaction: $F_{1,3} = 31.1$, $P = 0.011$; the analyses of responses by dominant steelhead are based on seven observations rather than eight because two fish

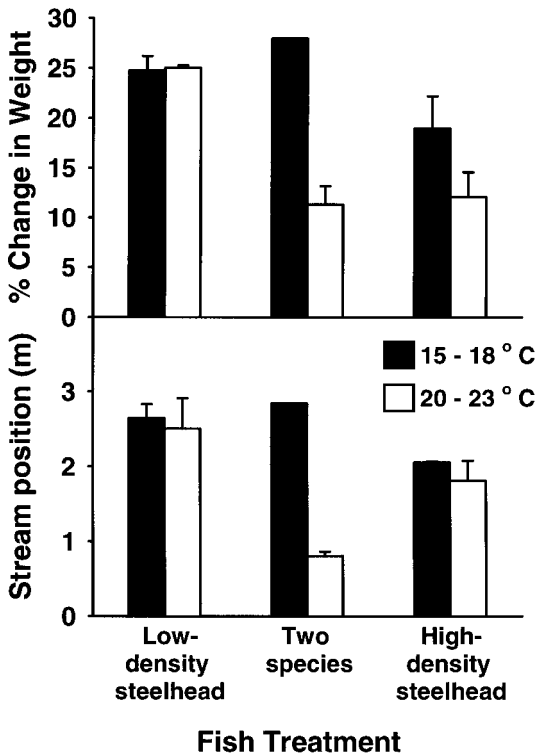


FIGURE 1.—Means (+SE) for growth (% change in weight) and stream position (meters from the upstream end of experimental stream units) of dominant juvenile steelhead in artificial streams under two temperature regimes and three different fish treatments. The low-density treatment used four steelhead, the high-density treatment eight steelhead, and the two-species treatment four steelhead and four Sacramento pikeminnow. The experimental units were 5.6 m long; a stream position of 0 represents the upstream end of a unit.

competed for dominance over one entire trial). All dominant steelhead survived. The stream positions of dominant steelhead in the low-density steelhead and two-species treatments corresponded with their patterns of growth in those treatments. Dominant steelhead were positioned 2 m further upstream in the two-species treatment in warm water compared with their positions in the two-species treatment in cool water and the low-density steelhead treatments under either thermal regime (Figure 1; ANOVA of fish treatment \times temperature interaction: $F_{1,3} = 10.7$, $P = 0.047$). Because dominant steelhead generally maintained positions upstream of all other fish, this difference in position indicates that dominant steelhead were able to defend only a relatively small area in warm water when Sacramento pikeminnow were present.

The contrast between the high-density and

two-species treatments indicated that Sacramento pikeminnow and additional steelhead similarly affected the growth of dominant steelhead in warm water; growth of dominant steelhead was lower in warm water, independent of species composition (Figure 1; ANOVA: $F_{1,3} = 13.5$, $P = 0.035$). In contrast, in warm water Sacramento pikeminnow affected the stream position of dominant steelhead even more than an equal number of steelhead; dominant steelhead occupied positions relatively far upstream in the two-species treatment in warm water compared with high-density steelhead treatments and the two-species treatment in cool water (Figure 1; ANOVA of fish treatment \times temperature interaction: $F_{1,3} = 25.3$, $P = 0.015$).

For subdominant steelhead, the contrast of the two-species and low-density steelhead treatments revealed variable growth and survival within treatments and no detectable effects of temperature, the presence of Sacramento pikeminnow, or their interaction (Figure 2; MANOVA: $df = 1, 4$; all $P > 0.26$). Subdominant steelhead were on average 0.5 m further upstream in warm water than in cool water (Figure 2; ANOVA: $F_{1,4} = 5.89$, $P = 0.094$), but their position was not affected by the presence of Sacramento pikeminnow ($F_{1,4} = 0.03$, $P = 0.878$) nor the interaction of fish treatment \times temperature ($F_{1,4} = 1.57$, $P = 0.299$). Growth and survival of Sacramento pikeminnow were also independent of temperature (MANOVA: $F_{1,2} = 3.83$, $P = 0.190$), but the position of Sacramento pikeminnow averaged 2.7 m further upstream for trials in warmwater compared with coolwater (t -test: $df = 2$, $P = 0.061$).

The contrast between the high-density steelhead and two-species treatments revealed higher growth and survival of subdominant steelhead in the presence of Sacramento pikeminnow than in the presence of an equal density of steelhead (Figure 2; MANOVA: $F_{1,4} = 24.20$, $P = 0.016$), but growth and survival were independent of temperature (MANOVA: $F_{1,4} = 5.22$, $P = 0.110$) and the interaction of fish treatment \times temperature (MANOVA: $F_{1,4} = 0.85$, $P = 0.420$). Subdominant steelhead also occupied positions relatively far upstream in the two-species treatment in warm water, probably in response to the upstream position of dominant steelhead (Figure 2; ANOVA of interaction of fish treatment \times temperature: $F_{1,4} = 13.8$, $P = 0.021$). However, this result is confounded by the fact that mean position of subdominant fish in the high-density steelhead treatments summarizes the position of seven subdominant steelhead, whereas the two-

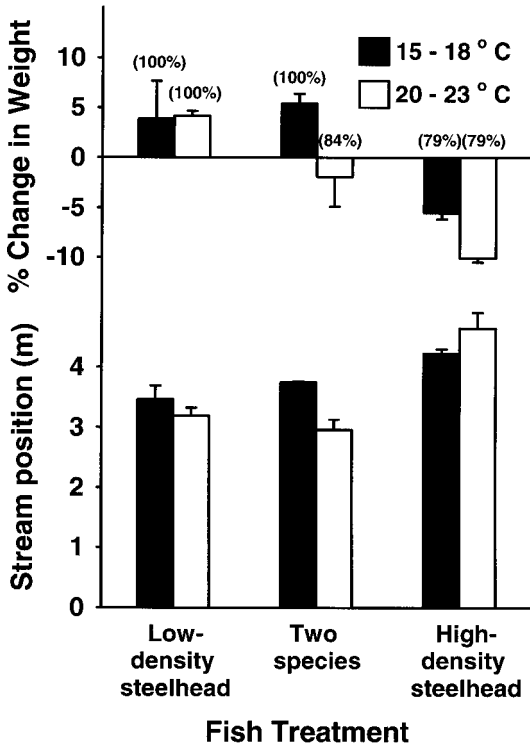


FIGURE 2.—Means (\pm SE) for growth (% change in weight) and stream position of subdominant juvenile steelhead in artificial streams under two temperature regimes and three different fish treatments. Data in parentheses above the bars for change in weight indicate mean survival in two replicate trials.

species treatments contained only three subdominant steelhead (except in the two-species trial where no dominant steelhead was apparent and only two steelhead were clearly subdominant).

Predictably, growth related to stream position differed for dominant steelhead and subdominant steelhead. Dominant steelhead positioned downstream grew more than those positioned upstream ($r^2 = 0.69$, $df = 10$, $P < 0.01$). Dominant fish in favorable conditions (e.g., the two species treatment in cool water) positioned themselves near the downstream end of the food delivery device. In contrast, subdominant steelhead positioned farther upstream fared better than those downstream ($r^2 = 0.27$, $df = 11$, $P = 0.048$). Like subdominant steelhead, Sacramento pikeminnow grew faster in trials where they were able to maintain upstream positions ($r^2 = 0.89$, $df = 3$, $P = 0.038$). All of these results are confounded by differences in water temperature, and results for subdominant steel-

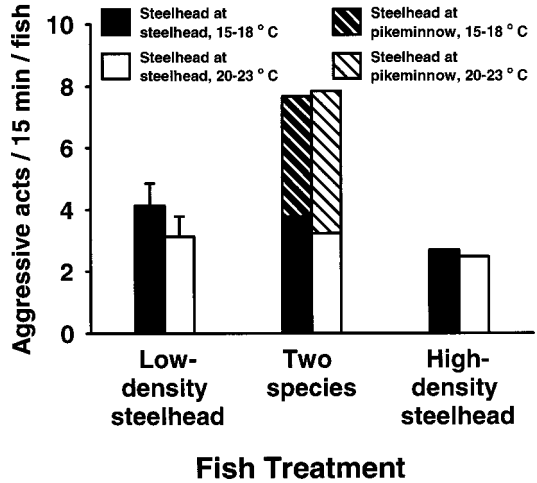


FIGURE 3.—Aggressive behavior by steelhead in artificial streams toward conspecifics and Sacramento pikeminnow under two temperature regimes and three different fish treatments. Error bars indicate SEs with $N = 2$ using means from observations of separate trials. Behavioral observations were made on only one replicate for the two-species and high-density treatments.

head are further confounded by differing numbers of individuals among treatments.

Inspection of the behavior data also supports the hypothesis that interactions between juvenile steelhead and Sacramento pikeminnow are sensitive to temperature. Although intraspecific aggressive behavior by steelhead appeared to be similar across all treatments, the presence of Sacramento pikeminnow increased the total number of aggressive acts by steelhead (Figure 3). In the two-species treatment at both temperatures, steelhead directed about equal numbers of aggressive acts (primarily “nips” and “threat nips” sensu Hartman 1965) toward conspecifics and Sacramento pikeminnow. The overall rate of aggressive behavior by steelhead appeared similar in cool and warm water for the two-species treatment. In warm water, however, dominant steelhead performed most of the aggressive acts toward Sacramento pikeminnow, but in cool water subdominant steelhead performed most of the interspecific aggressive acts. In the upper third of the experimental units, which was almost always occupied by the dominant steelhead, steelhead initiated aggressive acts on Sacramento pikeminnow in warm water at about twice the rate recorded for cool water. Dominant steelhead were unable to displace Sacramento pikeminnow from the upstream portion of the experimental units in two-species trials in warm water, but Sacramento pikeminnow in cool water

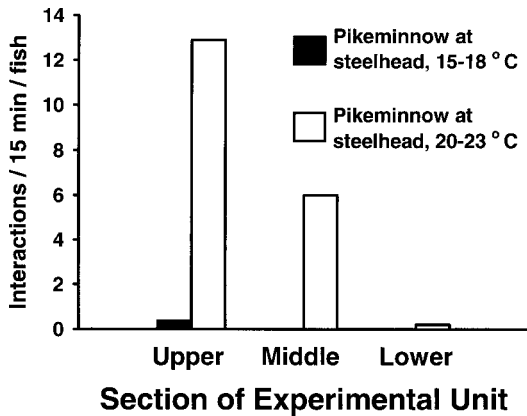


FIGURE 4.—Means of behavioral interactions directed toward steelhead by Sacramento pikeminnow at two temperatures in artificial streams.

usually occupied more downstream positions and thus overlapped more extensively with subdominant steelhead. On the rare occasions when Sacramento pikeminnow in cool water moved into the upstream portions of the experimental units, they usually sought cover and did not feed.

Sacramento pikeminnow interacted with steelhead about 50 times more often in warm water compared with cool water (Figure 4). Behavioral interactions by Sacramento pikeminnow consisted almost entirely of evictions and parallel displays (as described by Reeves [1984] for reddsides shiners). Interactions with steelhead initiated by Sacramento pikeminnow were always associated with attempts to capture specific prey items, which is reflected in the distribution of their activity within the experimental units (Figure 4). Sacramento pikeminnow did not attempt to exclude other fish from feeding areas and did not develop dominance hierarchies. Steelhead involved in interactions initiated by Sacramento pikeminnow would often remain close to their previous position and were not harassed repeatedly.

Discussion

This experiment suggests that juvenile Sacramento pikeminnow have negligible effects on the growth of dominant juvenile steelhead in water 15–18°C, but the effect of juvenile Sacramento pikeminnow on the growth of dominant juvenile steelhead at 20–23°C is about equal to the effect of additional juvenile steelhead. To our knowledge, previous research on the temperature-dependence of interactions between stream fishes has not contrasted interspecific and intraspecific effects. However, our

results coincide with research suggesting that water temperature can influence interactions among stream fishes (Baltz et al. 1982; Cunjak and Green 1986; Reeves et al. 1987; De Staso and Rahel 1994; Taniguchi et al. 1998). Our results also correspond with previous studies that found no evidence of negative effects of cyprinids on stream salmonids in water temperatures of 15–18°C or lower (Symons 1976; Grossman and Boulé 1991).

Sacramento pikeminnow and steelhead had similar per capita effects on the growth of dominant juvenile steelhead in warm water, but dominant steelhead interacted much differently with Sacramento pikeminnow than they did with conspecifics. In all trials, steelhead maintained territories that they defended against conspecifics; aggressive interactions among steelhead usually involved the displacement of the less dominant individual. Sacramento pikeminnow were not territorial and responded to aggressive acts by steelhead with only localized movements. The high level of activity by Sacramento pikeminnow in warm water and their failure to respect the territories of steelhead allowed them to compete exploitatively for food with dominant steelhead. Reeves et al. (1987) found that another cyprinid, the reddsides shiner, interacted similarly with steelhead in water 19–22°C. In response to competition from Sacramento pikeminnow, dominant steelhead occupied positions further upstream in the experimental units than they did in the high-density steelhead treatment. Although this change in position had little or no energetic cost because of the relatively uniform water velocities in the experimental units, such a change in position in natural streams might require that steelhead occupy microhabitats with higher water velocities. This raises the possibility that the per capita effects of Sacramento pikeminnow on dominant steelhead in warm water could exceed intraspecific competition. Depending on the body sizes of sympatric Sacramento pikeminnow, steelhead in the Eel River may shift to faster water in response to competition, increased predation risk (Brown and Moyle 1991), or both processes.

Substantial within-treatment variation and minimal replication combined to obscure any effects of Sacramento pikeminnow on subdominant steelhead. However, the clear influence of temperature on the behavior of Sacramento pikeminnow suggests that they are more likely to affect subdominant steelhead in warm water. The relative effect of intraspecific competition versus interspecific competition on subdominant steelhead may have

been overestimated because, the artificial stream did not allow subdominant fish to emigrate or readily avoid interactions with conspecifics.

We believe the results of this experiment are relevant to the natural system because the treatments represented temperature regimes commonly encountered within the range of steelhead in the Eel drainage and because the natural relative densities of Sacramento pikeminnow in this drainage often exceed the 1:1 ratio we used in the experiment (Brown and Moyle 1997; B. C. Harvey, unpublished data). Tributaries of the Eel River with summer water temperatures averaging around 20–23°C at the warmest time of the year can contain relatively high densities of juvenile steelhead (Harvey, unpublished data). Similarly, extensive longitudinal censuses of a tributary of the South Umpqua River in southern Oregon revealed relatively high densities of juvenile steelhead in downstream reaches where afternoon water temperatures commonly reached 20–22°C (Roper et al. 1994). These field observations are supported by laboratory studies that have measured substantial growth of rainbow trout *Oncorhynchus mykiss* at 22°C and have shown that the warm temperature treatment in our experiment is substantially lower than the critical thermal maxima (>28°C) for some strains of rainbow trout acclimated to warm temperatures (Myrick and Cech 2000). Thus, the warm temperature treatment in the experiment duplicated temperatures at which steelhead can achieve significant densities. However, our observations may be less germane to interactions between the species within parts of their native ranges where stream reaches with water temperatures in the 20–23°C range may be of less significance to steelhead or rainbow trout.

Although the effects of piscivorous adult pikeminnow on juvenile salmonids have received substantial attention, this study suggests that competition between smaller Sacramento pikeminnow and steelhead also deserves consideration by resource managers. The two species may compete both in large channels inhabited by large (adult) Sacramento pikeminnow and in smaller streams rarely occupied by adult pikeminnow. Efforts to restore cooler thermal regimes to smaller stream channels may particularly benefit salmonids in drainages containing Sacramento pikeminnow by reducing the extent of overlap between the taxa and by reducing the rates of interspecific competition and predation on steelhead where overlap does occur.

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References

- Baltz, D. M., P. B. Moyle, and N. J. Knight. 1982. Competitive interactions between benthic stream fishes, riffle sculpin, (*Cottus gulosus*), and the speckled dace, (*Rhinichthys osculus*). *Canadian Journal of Fisheries and Aquatic Sciences* 39:1502–1511.
- Beamesderfer, R. C. P., D. L. Ward, and A. A. Nigro. 1996. Evaluation of the biological basis for a predator control program on northern squawfish (*Ptychocheilus oregonensis*) in the Columbia and Snake rivers. *Canadian Journal of Fisheries and Aquatic Sciences* 53:2898–2908.
- Brown, L. R., and A. M. Brasher. 1995. Effects of predation by Sacramento squawfish (*Ptychocheilus grandis*) on habitat choice of California roach (*Lavinia symmetricus*) and rainbow trout (*Oncorhynchus mykiss*) in artificial streams. *Canadian Journal of Fisheries and Aquatic Sciences* 52:1639–1646.
- Brown, L. R., and P. B. Moyle. 1991. Changes in habitat and microhabitat partitioning within an assemblage of stream fishes in response to predation by Sacramento squawfish (*Ptychocheilus grandis*). *Canadian Journal of Fisheries and Aquatic Sciences* 48:849–856.
- Brown, L. R., and P. B. Moyle. 1997. Invading species in the Eel River, California: successes, failures, and relationships with resident species. *Environmental Biology of Fishes* 49:271–291.
- Cech, J. J., Jr., S. J. Mitchell, D. T. Castleberry, and M. McEnroe. 1990. Distribution of California stream fishes: influence of environmental temperature and hypoxia. *Environmental Biology of Fishes* 29:95–105.
- Cunjak, R. A., and J. M. Green. 1986. Influence of water temperature on behavioural interactions between juvenile brook charr, *Salvelinus fontinalis*, and rainbow trout, *Salmo gairdneri*. *Canadian Journal of Zoology* 64:1288–1291.
- De Staso, J., III, and F. J. Rahel. 1994. Influence of water temperature on interactions between juvenile Colorado River cutthroat trout and brook trout in a laboratory stream. *Transactions of the American Fisheries Society* 23:289–297.
- Grossman, G. D., and V. Boulé. 1991. Effects of rosyside dace (*Clinostomus funduloides*) on microhabitat use of rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 48:1235–1243.
- Hartman, G. F. 1965. The role of behavior in the ecology and interaction of underyearling coho salmon (*O-*

- corhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 22:1035–1081.
- Hartman, K. J., and S. B. Brandt. 1995. Comparative energetics and the development of bioenergetics models for sympatric estuarine predators. Canadian Journal of Fisheries and Aquatic Sciences 52:1647–1666.
- Harvey, B. C., J. L. White, and R. J. Nakamoto. 2002. Habitat relationships and larval drift of native and nonindigenous fishes in neighboring tributaries of a coastal California river. Transactions of the American Fisheries Society 131:159–170.
- Knutsen, C. J., and D. L. Ward. 1999. Biological characteristics of northern pikeminnow in the lower Columbia and Snake rivers before and after sustained exploitation. Transactions of the American Fisheries Society 128:1008–1019.
- Moyle, P. B., and T. Light. 1996a. Fish invasions in California: do abiotic factors determine success? Ecology 77:1666–1670.
- Moyle, P. B., and T. Light. 1996b. Biological invasions of fresh water: empirical rules and assembly theory. Biological Conservation 78:149–161.
- Moyle, P. B., and J. E. Williams. 1990. Biodiversity loss in the temperate zone: decline of the native fish fauna of California. Conservation Biology 4:275–284.
- Myrick, C. A., and J. J. Cech, Jr. 2000. Temperature influences on California rainbow trout physiological performance. Fish Physiology and Biochemistry 22: 245–254.
- Reeves, G. H. 1984. Interactions between redbside shiner (*Richardsonius balteatus*) and the steelhead trout (*Salmo gairdneri*) in western Oregon: the influence of water temperature. Doctoral dissertation. Oregon State University, Corvallis.
- Reeves, G. H. 1988. A food delivery system for laboratory streams. Canadian Journal of Fisheries and Aquatic Sciences 66:755–758.
- Reeves, G. H., F. H. Everest, and J. D. Hall. 1987. Interactions between the redbside shiner (*Richardsonius balteatus*) and the steelhead trout (*Salmo gairdneri*) in western Oregon: the influence of water temperature. Canadian Journal of Fisheries and Aquatic Sciences 44:1603–1613.
- Reeves, G. H., F. H. Everest, and C. E. McLemore. 1983. A recirculating stream aquarium for ecological studies. U.S. Forest Service Research Note PNW-403.
- Roper, B. B., D. L. Scarnecchia, and T. J. La Marr. 1994. Summer distribution and habitat use by chinook salmon and steelhead within a major basin of the South Umpqua River, Oregon. Transactions of the American Fisheries Society 123:298–308.
- Symons, P. E. K. 1976. Behavior and growth of juvenile Atlantic salmon (*Salmo salar*) and three competitors at two stream velocities. Journal of the Fisheries Research Board of Canada 33:2766–2773.
- Taniguchi, Y., F. J. Rahel, D.C. Novinger, and K. G. Gerow. 1998. Temperature mediation of competitive interactions among three fish species that replace each other along longitudinal stream gradients. Canadian Journal of Fisheries and Aquatic Sciences 55:1894–1901.
- White, J. L., and B. C. Harvey. 2001. Effects of an introduced piscivorous fish on native benthic fishes in a coastal river. Freshwater Biology 46:987–995.
- Zimmerman, M. P. 1999. Food habits of smallmouth bass, walleyes, and northern pikeminnow in the lower Columbia River basin during outmigration of juvenile anadromous salmonids. Transactions of the American Fisheries Society 128:1036–1054.
- Zimmerman, M. P., and D. L. Ward. 1999. Index of predation on juvenile salmonids by northern pikeminnow in the lower Columbia River basin, 1994–1996. Transactions of the American Fisheries Society 128:995–1007.