

AN EMERGENT MULTIPLE PREDATOR EFFECT MAY ENHANCE BIOTIC RESISTANCE IN A STREAM FISH ASSEMBLAGE

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Abstract. While two cyprinid fishes introduced from nearby drainages have become widespread and abundant in the Eel River of northwestern California, a third nonindigenous cyprinid has remained largely confined to ≤ 25 km of one major tributary (the Van Duzen River) for at least 15 years. The downstream limit of this species, speckled dace, does not appear to correspond with any thresholds or steep gradients in abiotic conditions, but it lies near the upstream limits of three other fishes: coastrange sculpin, prickly sculpin, and nonindigenous Sacramento pikeminnow. We conducted a laboratory stream experiment to explore the potential for emergent multiple predator effects to influence biotic resistance in this situation. Sculpins in combination with Sacramento pikeminnow caused greater mortality of speckled dace than predicted based on their separate effects. In contrast to speckled dace, 99% of sculpin survived trials with Sacramento pikeminnow, in part because sculpin usually occupied benthic cover units while Sacramento pikeminnow occupied the water column. A 10-fold difference in benthic cover availability did not detectably influence biotic interactions in the experiment. The distribution of speckled dace in the Eel River drainage may be limited by two predator taxa with very different patterns of habitat use and a shortage of alternative habitats.

Key words: biotic resistance; Cottidae; cover; Cyprinidae; emergent multiple predator effects; introduced species; laboratory stream; predation risk; stream fish.

INTRODUCTION

The ability of communities to resist invasion is a significant issue in community ecology and resource management (Mack et al. 2000). While empirical rules for predicting invasion resistance are available for some taxa (e.g., Moyle and Light 1996a), the generality of these rules remains unclear. For example, previous studies of invasion resistance in California stream fish communities have emphasized the importance of the physical environment. Moyle and Light (1996b) suggested that for invading fishes in California streams, “if abiotic factors are appropriate for an exotic species, then that species is likely to successfully invade, regardless of the biota already present.” Baltz and Moyle (1993) concluded that the natural hydrologic regime was the key element that prevented invasion of Deer Creek, California by nonindigenous fishes. So does a match between the habitat requirements of an invading species and the receiving system dictate a successful invasion, or might biotic resistance also be significant in some circumstances? While patterns of resource use by fishes in Deer Creek did not support the hypothesis of resistance to invasion via competition, Baltz and Moyle (1993) noted that predation might be a significant contributor to invasion resistance. Predation-driven invasion resistance occurs in other aquatic systems,

although such resistance may be limited to specific habitats or otherwise affect patterns in the abundance but not the large-scale distribution of invaders (e.g., Robinson and Wellborn 1988, Reusch 1998, Byers 2002).

Emergent multiple predator effects may influence the degree of biotic resistance in some communities. Emergent multiple predator effects occur when the combined effect of multiple predators on prey differs from that predicted using the predators’ separate effects (Sih et al. 1998). For example, facilitation among predators, which could enhance invasion resistance, might be predicted where predators utilize different habitats such that prey lack physical refuges. Eklöv and VanKooten (2001) observed such facilitation in the effect of perch (*Perca fluviatilis*) and northern pike (*Esox lucius*) on roach (*Rutilus rutilus*) in pond enclosures containing both open water and vegetated habitat. Yellow perch are more effective predators in open water, while northern pike are more efficient than yellow perch in physically complex habitats.

In general, patterns in the success of invasion by stream fishes in the Eel River of northwestern California appear to follow Moyle and Light’s (1996b) assertion that, in California streams, correspondence between the physical habitat requirements of invading species and the available habitat determines invasion success. For example, the two nonindigenous species with broad distributions and relatively high densities in the Eel River drainage are cyprinids native to nearby drainages offering similar physical conditions (Brown

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PLATE 1. Sacramento pikeminnow swimming over cover units in the artificial stream. Photo by R. J. Nakamoto.

and Moyle 1997): both the California roach (*Lavinia symmetricus*) and the Sacramento pikeminnow (*Ptychocheilus grandis*) became widespread in the Eel drainage within 10 years of their introductions (in about 1970 for California roach and 1980 for Sacramento pikeminnow, both by unknown means). However, a third cyprinid also native to adjacent drainages, the speckled dace (*Rhinichthys osculus*), does not fit this pattern.

Since its introduction into the Eel River drainage before 1988 (Brown and Moyle 1997), the speckled dace has remained confined to one major tributary (the Van Duzen River). With the exception of rare captures 5–10 km downstream, most recently a total of two individuals 5 km downstream in annual collections during 1996–2002 (B. C. Harvey, J. L. White, and R. J. Nakamoto, *unpublished data*), the downstream extent of the species' range has remained constant since 1987. While a physical barrier defines the upstream limit of the current 25-km range of speckled dace in the Van Duzen River, its downstream limit appears unrelated to physical factors. For example, maximum weekly mean temperature over 1 year at the downstream limit of speckled dace in the Van Duzen River and at a site 20 km downstream differed by only 0.2°C (J. L. White, *unpublished data*). However, the downstream limit of speckled dace lies just upstream of the upper limit of both coastrange sculpin (*Cottus aleuticus*) and prickly sculpin (*C. asper*). These native sculpins commonly occupy habitats with coarse substrates that speckled dace also prefer (Moyle 2002). The upstream extent of the distribution of Sacramento pikeminnow and downstream extent of speckled dace in the Van Duzen River overlap by about 15 km, although Sacramento pikeminnow are rare in that reach. In contrast to speckled dace, neither California roach nor Sacramento pikeminnow faced ecologically similar species or potentially significant predation risk from the depauperate Eel River fish assemblage (described in Brown and Moyle 1997).

Along with the patterns in fish distributions in the Van Duzen River, other observations suggest that biotic interactions could be important in determining the distribution of speckled dace in the Eel River drainage. Competition for space with riffle sculpin (*C. gulosus*) influenced the habitat use of speckled dace in Deer Creek, California: In a reach where riffle sculpin were rare, speckled dace tended to occupy fast water with coarse substrates, but where riffle sculpin were abundant, speckled dace occupied slower water at the stream margins (Baltz et al. 1982). Riffle sculpin also consumed speckled dace during laboratory experiments by Baltz et al. (1982), and piscivory by sculpins has been observed frequently (Moyle 2002). As adults, Sacramento pikeminnow are largely piscivorous, consuming a wide variety of fishes including benthic species (e.g., Brown and Moyle 1997, White and Harvey 2001). Given these observations, we hypothesized that competition for space and predation by sculpins in benthic habitat, combined with predation by Sacramento pikeminnow, which occupy the water column, could lead to an emergent multiple predator effect on speckled dace. We tested this hypothesis in a large artificial stream. We also included the availability of benthic cover as a factor in the experiment, because it is likely to affect the predator–prey interactions of interest and because its availability in the Eel River drainage is heterogeneous in space and time.

METHODS

We conducted the experiment from 2 January 2001 to 6 June 2001 in a recirculating laboratory stream with a channel 0.30–0.75 m wide and a total area of 7.1 m², with water depth of 45–50 cm and gravel substratum. A Plexiglas inner wall allowed observation of the entire stream. Electric pumps produced mean water velocities of 35 cm/s in the narrow part of the channel and 14 cm/s in the remainder. Water temperature was maintained at 16°–17°C.

Artificial lights provided 10 h of light per day, augmented by limited natural light from windows along two sides of the stream.

The experiment included two levels of three cross-classified factors: Sacramento pikeminnow (absent or three individuals, 315–419 mm standard length [SL; from anterior end of head to posterior end of vertebral column]; see Plate 1), sculpin (absent or 10 individuals, 59–112 mm SL, five *C. asper*, and five *C. aleuticus*), and benthic cover (3 or 30 units constructed of two black plastic panels 30 × 18 cm, held 2 cm apart by two 12-cm-long spacers). The number of Sacramento pikeminnow we used produced a density (0.4 fish/m²) approaching the maximum we have observed in the Van Duzen River (0.5 fish/m²) for entire mesohabitats (B. C. Harvey, *unpublished data*). We selected this density in part because our observations of piscivory by Sacramento pikeminnow indicated they commonly feed in groups. We used a sculpin density (1.4 fish/m²) that we estimated was similar to the density in riffles at the upstream limit of sculpins in the Van Duzen River. Sculpin densities in riffles 5–10 km below their upstream limit were 0.6–1.2 fish/m² in 2001 (J. L. White, *unpublished data*). Sculpin density in a short reach that included both a pool and a riffle about 20 km below the upstream limit averaged 0.6 fish/m² over 3 yr (Brown et al. 1995). We attempted to use a size distribution of sculpin in each trial that approximately matched field data from multiple sampling sites on the Van Duzen River. The survival of 10 speckled dace (39–70 mm SL) provided the main response variable. The entire artificial stream was used for each trial, and the order of treatments randomized. We completed five replicates of each treatment combination, except for the two treatments lacking either predator, which were replicated three times. We obtained fish for the experiment from nearby rivers by seining, hand netting, and electrofishing. Both sculpins and speckled dace were collected from sites where predators that commonly occupy the water column, such as Sacramento pikeminnow and adult cutthroat trout (*Oncorhynchus clarkii*), were rare. Fish were held in laboratory tanks with the same water temperature as the artificial stream for at least 7 d before being used in the experiment. During this period, we fed Sacramento pikeminnow various cyprinids while sculpins and speckled dace received frozen brine shrimp (*Artemia* spp.), tubificid worms, and benthos collected from nearby streams.

Each trial began with the addition of sculpins and speckled dace to the artificial stream on the morning of day 1, followed by Sacramento pikeminnow on the morning of day 2. We censused the number of surviving speckled dace at the conclusion of each trial on the morning of day 3. Fish were haphazardly selected for use in individual trials; some Sacramento pikeminnow and sculpins were used in multiple trials, but speckled dace were not. For 29 trials, we observed the distribution of fishes on the morning of day 2 before Sac-

ramento pikeminnow were added to the two predator treatments that included them, and before concluding each trial on day 3. For 28 trials, we also made observations of fish on the evening of day 2. From these observations, we: (1) quantified the use of benthic cover by both speckled dace and sculpins; and (2) generated minimum estimates of movement beneath and among benthic cover units by speckled dace and sculpins while Sacramento pikeminnow were present, by comparing their distributions on the evening of day 2 and the morning of day 3. These minimum estimates of movement were generated only from differences in the number of fish beneath specific cover units; we did not identify individual fish. We weighed and measured speckled dace and sculpins before each trial and weighed and measured surviving fish at the end of each trial. We used the change in weight of sculpin to quantify their consumption of speckled dace.

We analyzed the survival of speckled dace using log-transformed data in a three-way ANOVA with Sacramento pikeminnow, sculpin, and benthic cover as main effects. With log-transformed data, the interaction term for the two predators tests the multiplicative model of multiple predator effects, in which the predicted effect of two predators in combination is $Pr_a + Pr_b - (Pr_a Pr_b)$, where Pr_a and Pr_b represent the effects of the two predators alone (Soluk and Collins 1988, Sih et al. 1998). The simpler additive model (where the predicted effect of the two predators = $Pr_a + Pr_b$) is not appropriate in this case because that model includes prey that would be killed twice (the $Pr_a Pr_b$ term in the multiplicative model) in situations where prey depletion occurs.

We analyzed the use of cover by speckled dace and sculpins with two-way ANOVA. For speckled dace, we analyzed the effect of predator treatment (Sacramento pikeminnow or sculpin) and cover availability on the change in use of cover during the trials, by using as a response variable the difference between use of cover at the end of each trial and use of cover at the beginning of day 2, before Sacramento pikeminnow were added in trials that received them. The combined predator treatment could not be included in this analysis because survival of speckled dace in that treatment was not adequate to yield meaningful data on use of cover. We similarly analyzed use of cover by sculpins, except that the analysis could only include the two predator treatments that included sculpin. Finally, we inspected the minimum estimates of movement beneath and among cover units by speckled dace and sculpins while Sacramento pikeminnow were present to determine if movement might affect the interactions of interest.

RESULTS

Sacramento pikeminnow and sculpin consumed similar proportions (22–32%) of speckled dace when tested separately in the artificial stream. While sculpin outnumbered Sacramento pikeminnow and were together with speckled dace during the trials for twice as long,

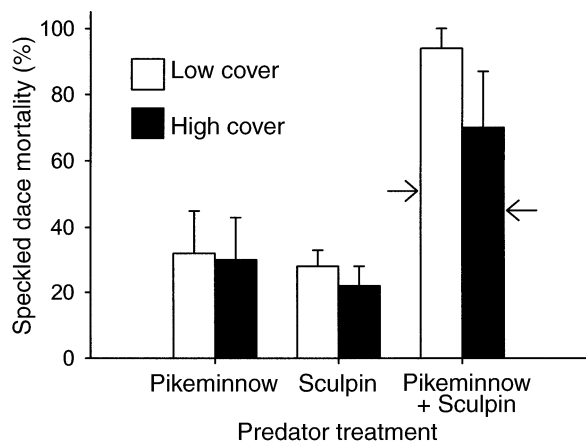


FIG. 1. Percentage mortality of speckled dace under three different predator treatments and two levels of benthic cover availability in an artificial stream experiment. (No mortality occurred in predator-free controls.) Arrows adjacent to bars representing the treatment with both Sacramento pikeminnow and sculpins indicate the predicted mortality rate assuming no emergent multiple predator effect. Error bars indicate ± 1 SE.

the size distribution of sculpin in each trial yielded only one or two individuals large enough to consume speckled dace. Only sculpin ≥ 94 mm SL consumed speckled dace in the experiment. Sacramento pikeminnow and sculpins in combination had a greater effect than that predicted using a multiplicative model of their separate effects (Fig. 1, Sacramento pikeminnow \times sculpin interaction, $F_{1,28} = 5.3$, $P = 0.03$), causing 94% mortality of speckled dace in the low cover treatment. The amount of benthic cover did not significantly influence the effects of the predators (for the cover effect and interactions involving cover, all $P > 0.28$). In sharp contrast to speckled dace, sculpins experienced high survival in the presence of Sacramento pikeminnow: we failed to recover only one of 100 sculpins from replicates of the combined-predator treatment. All speckled dace were recovered from predator-free trials.

Greater than predicted mortality of speckled dace in the combined-predator treatment resulted from higher predation rates by Sacramento pikeminnow but lower predation rates by sculpin compared to the single-predator trials. Sacramento pikeminnow consumed, on average, 3.1 speckled dace per trial in their single-predator treatment and 7.9 speckled dace per trial in the combined-predator treatment. Sculpin consumed, on average, 2.5 speckled dace per trial in their single-predator treatment but only 0.03 speckled dace per trial in the combined-predator treatment.

The use of benthic cover by both speckled dace and sculpin varied significantly among treatments (Fig. 2). In the Sacramento pikeminnow treatment, about one third of the speckled dace occupied benthic cover before the predator was added, but $>95\%$ of the surviving fish occupied benthic cover at the end of the trials. Less

than 2% of speckled dace occupied cover at any time during trials of the sculpin treatment. Thus, predator treatment had a strong effect on the change in use of cover during the trials by speckled dace ($F_{1,16} = 59.5$, $P < 0.0001$). This pattern was independent of cover availability (predator treatment \times cover interaction, $P = 0.41$); cover availability alone also did not affect changes in use of cover by speckled dace ($P = 0.62$). As many as eight speckled dace simultaneously occupied individual cover units. While use of cover averaged $>50\%$ at all times for sculpin (Fig. 2), the use of cover increased during trials, particularly in the combined predator treatment with low cover availability (predator treatment \times cover interaction, $F_{1,14} = 5.8$, $P = 0.03$). As many as five sculpin simultaneously occupied individual cover units.

Both speckled dace and sculpins moved beneath and among benthic cover units while Sacramento pikeminnow were present. The movement estimate for speckled dace in the Sacramento pikeminnow treatment was 10% with low cover availability and 40% with high cover availability. At least 27% of sculpin in the low cover, combined-predator treatment moved beneath or among cover units while Sacramento pikeminnow were present; at least 37% of sculpin did so in the high cover, combined-predator treatment. These movement estimates for sculpin in the presence of Sacramento pikeminnow paralleled movement estimates for sculpin in trials without Sacramento pikeminnow, which averaged 30%.

DISCUSSION

The combination of sculpins and Sacramento pikeminnow resulted in an enhancement of predation risk for speckled dace in the artificial stream compared to the expected risk based on the predators' separate effects. This form of emergent multiple predator effect is expected where appropriate predator-specific responses by prey conflict, for example where predators occupy and forage in different habitats (Sih et al. 1998, Eklöv and VanKooten 2001). For the species in this experiment, strong differences in habitat use by the two predators suggest that higher densities of either of the two predators alone probably would not result in risk for prey equal to that caused by the predators in combination. Benthic cover is probably an effective refuge for speckled dace from even high densities of Sacramento pikeminnow, while speckled dace can occupy the water column in the presence of sculpin. Differences in habitat use by the predators in this case are exacerbated by the predator-prey relationship between them: sculpin occupy cover more frequently in the presence of Sacramento pikeminnow (Fig. 2), and Sacramento pikeminnow strongly increase the risk of predation for sculpin in the field (White and Harvey 2001).

While a $10\times$ difference in the availability of cover did not detectably affect predation rates in our ex-

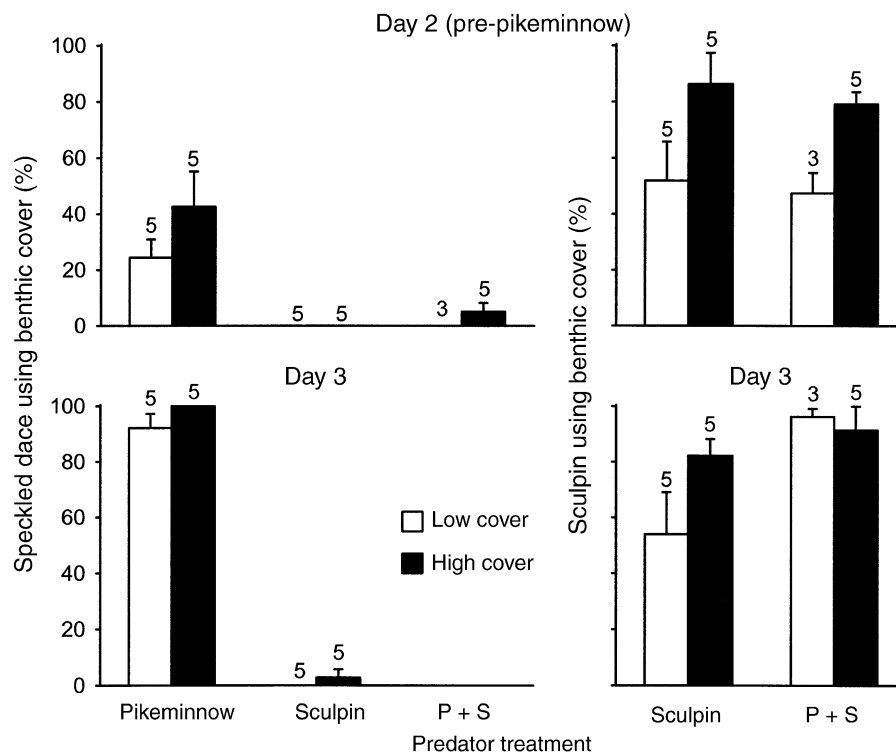


FIG. 2. Use of cover by speckled dace and sculpins under different predator treatments and two levels of benthic cover availability in an artificial stream experiment. Data reflect the percentage of surviving fish using cover. Day-2 observations (top) show use of cover before the addition of Sacramento pikeminnow; day-3 observations (bottom) indicate use of cover one day after the addition of Sacramento pikeminnow (except for the sculpin-only predator treatment). Error bars indicate +1 SE. Numbers above bars indicate sample sizes (number of trials). No day-3 data are presented for speckled dace in the combined predator treatment because more than two fish survived in only 1 of 10 trials.

periment, we cannot conclude that the amount of cover is irrelevant in the natural system. For example, cover reduces the risk of predation by Sacramento pikeminnow for sculpins (White and Harvey 2001); Sacramento pikeminnow would be expected to greatly reduce the abundances of both sculpins and speckled dace in the absence of any cover. At the other extreme, abundant cover across mesohabitats might provide speckled dace with sculpin-free refuges from predation by Sacramento pikeminnow. Speckled dace apparently coexisted with relatively high densities of riffle sculpin in Deer Creek, California, by shifting to habitats with slower water velocities and coarse substrate (Baltz et al. 1982). We hypothesize that, in the high cover, combined-predator treatment in the artificial stream, movement among refuges by sculpin, and their subsequent displacement of speckled dace from those refuges, enhanced predation on speckled dace by Sacramento pikeminnow even when the availability of cover appeared excessive. Movement by sculpin in a natural system with benthic cover across a range of water velocities is probably not extensive enough to have the same effect. However, because of high fine-sediment loads, benthic cover is extremely rare in the Van Duzen River near the downstream limit

of speckled dace distribution, particularly in areas of low water velocity.

Discussion of differences between the artificial stream and natural systems raises additional questions about the relevance of this experiment to the distribution of speckled dace in the Van Duzen River. For example, the per capita risk for speckled dace in the artificial stream probably exceeded any natural system in which predators have alternative prey. The artificial stream also did not provide mesohabitats found in the natural system that might be relevant to the interactions studied. The Van Duzen River has large, shallow pools that commonly contain filamentous algae in the dry season. Sculpins and post-young-of-the-year Sacramento pikeminnow rarely occupy these pools, which therefore might provide habitat for speckled dace. Our experiment also did not address genetic constraints, which may influence the current distribution of speckled dace in the Van Duzen River. While the origin and initial size of the population in the Van Duzen River is unknown, a small number of founders seems likely. Reduced genetic diversity may inhibit invading populations through inbreeding depression or by limiting the ability to evolve (Sakai et al. 2001). Finally, the absence of examples of predation limiting the distri-

bution of introduced species in aquatic systems, and the apparent failure of very high predation rates to influence the distribution of an invading species (Robinson and Wellborn 1988), further suggest caution in concluding that predation alone limits the distribution of speckled dace in the Van Duzen River.

Freshwater fishes may commonly face a combination of piscivores in the water column and benthic, refuge-occupying piscivores and competitors. For example, Rahel and Stein (1988) observed inactivity in johnny darters (*Etheostoma nigrum*) in the presence of piscivorous smallmouth bass (*Micropterus dolomieu*), but johnny darter activity equal to 19% of control rates and lesser use of benthic cover by johnny darters in the presence of both smallmouth bass and refuge-occupying crayfish (*Orconectes rusticus*). Rahel and Stein hypothesized that this change in behavior increased the susceptibility of johnny darters to predation by smallmouth bass. Similarly, based on their observations in artificial streams, Bryan et al. (2002) suggested that predation risk for Little Colorado spinedace (*Lepidomeda vittata*) from rainbow trout (*Oncorhynchus mykiss*) is enhanced by the presence of crayfish (*Orconectes virilis*). However, these two laboratory studies did not detect consequences of these interactions on predation rates, and consequences of the behavioral changes they observed for natural populations have not been studied. Further study is needed to determine under what array of conditions facilitation between water-column predators and benthic competitors or predators has ecologically important consequences.

Several specific features of the situation we studied may contribute to biotic resistance to range expansion by speckled dace, if indeed biotic resistance is an important aspect of the natural system: (1) Sculpin both prey on speckled dace and compete with them for benthic cover (Baltz et al. 1982); (2) One consequence of the amphidromous life histories of the two sculpin species in the Eel River is that body size increases upstream (Brown et al. 1995). Thus, relatively large sculpin occupy the stream reach just downstream of speckled dace in the Van Duzen River, probably increasing the predation risk for small fishes in this reach. In fact, our experiment probably underestimated the predation risk for speckled dace from sculpin because the size distribution we used did not reflect the relative abundance of large individuals near the upstream limit of the sculpins' range. (3) While prickly and coastrange sculpin use similar habitat in the Eel River (Brown et al. 1995), differences in habitat use between these two species in another system (White and Harvey 1999) raise the possibility that the two sculpins in combination with Sacramento pikeminnow might lead to a greater effect on speckled dace than a combination of either sculpin species and Sacramento pikeminnow. One other potentially important aspect of the situation we studied is the order

of arrival of introduced species. Assuming that neither sculpins nor Sacramento pikeminnow alone could prevent range expansion by dace, if speckled dace had been introduced before Sacramento pikeminnow, they might have reached sculpin-free parts of the drainage before the combined effect of sculpins and Sacramento pikeminnow could limit their distribution. This may be an example where an introduced species has enhanced biotic resistance to invasion of the resident community, in contrast to observations that facilitation among invading species can be common (Simberloff and Von Holle 1999, Ricciardi 2001).

The commonness of emergent multiple predator effects and situations where biotic interactions prevent invasion remains to be determined. The tentative example in this paper does not greatly weaken Moyle and Light's (1996b) prediction that for California streams in general biotic resistance will not limit invading fishes. Resource managers need the ability to predict readily invaded communities, successful invaders, and their effects on ecosystems (Ricciardi and Rasmussen 1998, Mack et al. 2000). Results of this study suggest that, while community ecology theory may provide a useful framework for understanding biological invasions (Shea and Chesson 2002), particular results may be highly contingent on the organisms and ecosystems under consideration (Lawton 1999).

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