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RELATIONSHIP OF DIURNAL HABITAT USE OF NATIVE STREAM FISHES OF THE EASTERN GREAT BASIN TO PRESENCE OF INTRODUCED SALMONIDS

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ABSTRACT.—Introduced brown trout, *Salmo trutta,* are common to many streams of western North America. However, the ecological interactions between brown trout and native stream fishes are not well understood, particularly the nature and extent of antipredator responses of native species. We examined the effects of brown trout presence on diurnal habitat use by 2 small native fishes at a mesohabitat scale (e.g., pool, riffle, run, backwater, etc.). Adult and juvenile southern leatherside chub (*Lepidomeda aliciae,* formerly *Gila copei*) and juvenile mountain sucker (*Catostomus platyrhynchus*) were located in main channel pools in the absence of brown trout, but they were found almost exclusively in backwaters and cutoff pools (i.e., off-channel habitats) in streams where brown trout were abundant. Off-channel habitat appears to provide a refuge for native fishes in streams with abundant brown trout populations. Altered or degraded streams may not include sufficient off-channel refuge habitats to allow coexistence of native species and introduced brown trout.

Key words: invasive species, antipredator defenses, habitat shift, brown trout, Salmo trutta, Lepidomeda aliciae, Catostomus platyrhynchus.

Introduction of nonnative species has been recognized as one of the major causes of worldwide declines in native fish species diversity (Bruton 1995, Rahel 2002). In particular, introduced piscivorous fishes have strong negative effects on the density, geographic distribution, and persistence of native fish species (Moyle and Light 1996, Rahel 1997). For example, introduction of brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) in New Zealand precipitated the decline of several native fish species of the family Galaxiidae (Townsend 1996). Similarly, introductions of black bass (*Micropterus salmoides*) in North America have led to local loss of small fish species (Jackson 2002). Perhaps the most dramatic example is the introduction of Nile perch, *Lates niloticus,* in the East African great lakes, which led to the devastating decline and extinction of several native species of cichlids (Kaufman 1992, Ogutu-Ohwayo 1993). Despite the abundant examples of negative effects of introduced predatory fishes, the ecological interactions between native and introduced species and the ecological mechanisms behind declines of native species are poorly understood in most systems (Bruton 1995, Townsend 1996).

In addition to lethal effects of predators (i.e., direct consumption of prey), the mere presence of predators can induce antipredator defenses in surviving prey, such as changes in behavior, morphology, and life history (Tollrian and Harvell 1999). Although induced defenses decrease the probability of predation, they generate costs such as decreased growth, decreased energy available for reproduction, decreased hydrodynamic efficiency, etc. (Anholt and Werner 1999, Bronmark et al. 1999, Tollrian and Dodson 1999). One of the most common behavioral defenses in fish is induced change in habitat use. Habitats vary in risk of predation and resource availability often in a negative way (i.e., tradeoff between risk and reward). Occupation of low-risk habitats as a response to predators may result in reduced growth, fecundity, future reproduction, and survival. Little is known about induced defenses of native species to introduced predators; however, costs of nonlethal effects of predators may be substantial (Tollrian and Dodson 1999).

Habitat loss and degradation represent an additional threat to native species (Bruton 1995). Regulation of flow, channelization, pollution, and other human-caused impacts can

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reduce habitat complexity and lead to loss of refuge habitats. In this way threats from introduced species may be exacerbated by habitat loss and degradation (McIntosh 2000). Identifying interactions between nonlethal effects of introduced species and habitat degradation is important for understanding the overall impact of introduced predators on native species.

The Great Basin of the western USA has a long history of geographic isolation. Aquatic organisms in this basin have been semi-isolated from surrounding faunas for 10 to 27 million years (Hocutt and Wiley 1986). Habitat loss and effects of introduced predators have been implicated in the decline of several fish species native to the Great Basin (e.g., June sucker, *Chasmistes liorus*; Utah Lake sculpin, *Cottus echinatus*; and Tui chub, *Gila bicolor isolata;* Minckley and Deacon 1991). However, in most cases, the mechanisms by which habitat loss and introduced predators affect native species in the Great Basin are poorly understood.

Brown trout were introduced in the early 1900s to many streams and rivers of the Great Basin for recreational purposes. Brown trout can be highly piscivorous when introduced into streams with abundant populations of small native fish (Garman and Nielsen 1982, Zalewski et al. 1985), and they have been implicated in the decline of native species in other systems (Garman and Nielsen 1982, Townsend 1996, Penczak 1999). Although brown trout have been introduced widely in western North America, and many self-sustaining populations exist, little effort has been directed to understanding effects of introduced brown trout on populations of native stream fishes of the region.

The objective of this study is to determine patterns of diurnal habitat use of native stream fishes in relation to brown trout. Specifically, we examine behavioral shifts in habitat use by 2 native fish species in the presence of brown trout. We show that small stream fishes occupy different habitats when brown trout are present, and we suggest that these refuge habitats are only available in natural, non-channelized stream segments.

METHODS

To determine whether or not diurnal habitat use of native stream fishes varied in relation to the presence or absence of brown trout, we quantified habitat use of all native fish species in 6 stream segments in central Utah, USA. Habitat use was compared between 3 segments where brown trout were common and 3 segments where brown trout were rare or absent (no other trout species were present in stream segments where brown trout were absent). Surveys were conducted in fall 1998 (3 segments, 2 with brown trout and 1 without) and 1999 (3 segments, 1 with brown trout and 2 without) when water level and clarity were optimal for snorkel surveys. The 3 stream segments that contained high densities of brown trout were in Diamond Fork (2 segments) and Thistle Creek, Utah County. The 3 stream segments with few or no brown trout were in Salina Creek, Sevier County; San Pitch River, Sanpete County; and Sevier River near Circleville, Paiute County.

We used underwater observations to determine habitat use of fishes. Snorkel surveys were conducted by 1 or 2 individuals, depending on stream width, with additional personnel recording data (Heggenes et al. 1991). When fish were encountered, species, number observed, age class (adult or juvenile including young-of-year), and type of habitat occupied were recorded. Habitats were categorized as pool, riffle, or run for the main channel habitats, and backwater or cutoff pool for off-channel habitats. At the same time, habitats were mapped using standard surveying methods with a transit and stadia pole or handheld GPS systems to determine availability of habitat (calculated as percent total surface area) in each stream segment. We used a nonparametric, 2-sample test to compare differences between mean stream width and percent of surface area in off-channel habitat among streams with and without brown trout (Kruskal-Wallis, Proc NPAR1WAY; SAS 1988).

Although we encountered a total of 6 native species during surveys, only 2 species (southern leatherside chub and mountain sucker) were found in all 6 locations and could thus be used for comparative analyses. For purposes of analysis, we grouped habitats into main channel (pool, riffle, or run) or off-channel (backwater or cutoff pool) habitats. Differences in habitat use were quantified as the proportions of point locations in main channel or off-channel habitats. We used Fisher's exact test (SAS 1988) by species and age classes to determine

TABLE 1. Location, mean stream width, percent off-channel aquatic surface area, length of segment, and density of leatherside chub, mountain sucker, and brown trout in 6 stream segments.

Location	Mean stream width (m)	% off-channel surface area	Length of segment (m)	Leatherside chub/ 100 m	Mountain sucker/ 100 m	Brown trout/ 100 m
Diamond Fork 1	10.5	34	300	30.67	175	28.67
Diamond Fork 2	12.5	12	300	27	91	28.33
Thistle Creek	4.5	2	200	0.5	4.5	18
Salina Creek	4.3	3	300	9.33	26.33	3.67
San Pitch River	8.5	18	150	346.67	89.33	0
Sevier River	16	10	150	478	120	0

if the proportion of locations in the main channel differed between stream segments with and without brown trout. Point locations represented 1 or more individuals, but analyses were not weighted by number of individuals per location to avoid confounding differences in abundance among streams.

RESULTS

Study streams varied from about 4 m to 16 m mean stream width, with 2%–34% of surface area in off-channel habitats. However, there were no significant differences in mean stream width ($\chi^2_1 = 0.048$, $P = 0.83$) or percent of surface area in off-channel habitats ($\chi^2_1 = 0.047$, $P = 0.82$) between streams with and without brown trout (Table 1). Southern leatherside chub and mountain sucker were found at all 6 survey locations. We observed 350 adult southern leatherside chub (30 point locations), 1259 juvenile southern leatherside chub (29 point locations), 162 adult mountain sucker (55 point locations), and 1021 juvenile mountain sucker (46 point locations). In general, southern leatherside chub were more abundant in streams without brown trout; mountain sucker appeared about equally abundant in streams both with and without brown trout (Table 1). Other native fish encountered at 1 or more of the locations included mottled sculpin (*Cottus bairdi*), speckled dace (*Rhinichthys osculus*), redside shiner (*Richardsonius balteatus*), and cutthroat trout (*Oncorhynchus clarki*).

Habitat type occupied differed significantly for 3 of 4 species/age groups between streams with and without brown trout (Fig. 1). Adult and juvenile southern leatherside chub were found almost exclusively in off-channel habitats in the presence of brown trout compared to high occupancy of main channel habitats when brown trout were absent (adult southern leatherside chub, Fisher's exact test, $P = 0.0003$; juvenile southern leatherside chub, Fisher's exact test, $P = 0.00003$). Juvenile mountain sucker exhibited a similar shift away from use of main channel habitats when brown trout were present (Fisher's exact test, $P < 0.0001$). Adult mountain sucker exhibited approximately equal and high use of main channel habitats whether brown trout were present or absent (Fisher's exact test, $P = 0.08$).

DISCUSSION

Habitat shifts are a common response to the presence of a predator for many aquatic species (Schlosser 1987, Werner and Hall 1988, Fraser and Gilliam 1992, Eklov and Persson 1996). Stream fishes typically respond to the presence of a predator by avoiding the general area where the predator is located (Schlosser 1987, Fraser and Yip-Hoi 1995). Differential habitat use by prey in the presence of a predator is usually interpreted as an adaptive response to decreased mortality due to predation.

Even though stream fishes of the Great Basin have been isolated for an ecologically long time, they appear to exhibit a typical habitat shift in response to predators. Larger brown trout preferentially occupy main channel pools and runs (Heggenes 1988), probably because of increased food resource availability associated with flowing habitats (Fausch 1984). In streams with brown trout, southern leatherside chub and juvenile mountain sucker occupy off-channel habitats, such as backwaters and cutoff pools (Walser et al. 1999). In contrast, in streams without brown trout, southern leatherside chub and juvenile mountain sucker are more likely to be found in main channel pool

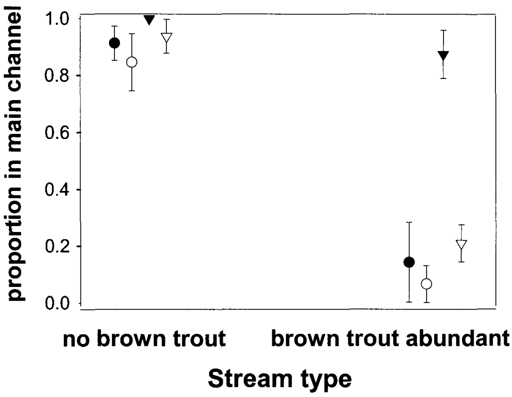

Fig. 1. Mean proportion (±1 $s_{\bar{x}}$) of juvenile and adult southern leatherside chub and mountain sucker found in the main channel (as compared to backwater and cutoff pool habitats) in streams with and without introduced brown trout. Adult southern leatherside chub = filled circles, juvenile southern leatherside chub = open circles, adult mountain sucker = filled triangles, juvenile mountain sucker = open triangles. In streams with no brown trout, all adult mountain sucker were located in main channel habitats, and so this mean has no variance.

and run habitats (Wilson and Belk 2001). Such habitat shifts may increase the probability of coexistence of vulnerable native species with introduced brown trout. Habitat shifts by southern leatherside chub and mountain sucker between streams cannot be explained by differences in habitat availability among streams. Although some streams have little off-channel habitat, there is no difference in availability between streams with or without brown trout (Table 1).

In contrast to southern leatherside chub and juvenile mountain sucker, adult mountain sucker exhibited no difference in habitat use in streams with or without brown trout. What differences in biology might account for this lack of habitat shift in adult mountain sucker? The most obvious explanation is that adult mountain sucker attain relatively large body sizes (up to 250 mm TL) compared to southern leatherside chub (up to 150 mm TL), and they may outgrow the threat of predation from gape-limited predators such as brown trout. Apparently, adult mountain sucker do not shift habitat use in the presence of brown trout because they are too large to be eaten by brown trout and thus do not perceive them as a threat.

Habitat plays an important role in interactions between predators and prey. Prey fishes typically shift to refuge habitats in the presence of a predator to decrease the risk of mortality (Gilliam and Fraser 1987, Brown and Moyle 1991, Chapman et al. 1996). Habitat diversity provides refugia for prey and opportunities for prey to reduce the threat of predation. However, degraded or simplified systems with little heterogeneity may lack refugia, and prey species may experience relatively high levels of predation. Thus, habitat degradation may exacerbate the negative effects of introduced predators (McIntosh 2000, Scott and Helfman 2001).

Some native fishes exhibited nearly exclusive use of off-channel habitats in the presence of brown trout in this study, suggesting that such habitats are important for coexistence. In channelized or degraded stream systems the amount of off-channel habitats may be reduced, eliminating potential refuge areas. Apparently, even with a high density of brown trout, native stream fishes are able to coexist if provided with sufficient refuge habitat. This interaction may explain why Wilson and Belk (2001) found only a weak relationship between the abundance of brown trout and occurrence of southern leatherside chub in the Sevier River system. Their data did not account for variation in habitat quality or extent of degradation among survey sites.

Occupation of refuge habitats may benefit native stream species by decreasing mortality, but species may incur costs as well. Prey fish occupying refuge habitats may experience decreased resource availability and increased competitive interactions within and between prey species (Mittelbach 1984, 1988). Decreased growth rates can lead to delayed maturity, decreased fecundity, and increased long-term risk of mortality (Anholt and Werner 1999, Bronmark et al. 1999, Tollrian and Dodson 1999). In this way nonlethal effects of brown trout on native species may result in additional population declines. Off-channel habitats may provide temporary refuge, but they may be inadequate for long-term viability of native species.

Results of this study have important implications for management of native stream fishes in areas where brown trout occur. Brown trout are strong predators on some native stream species (Nannini 2001). Minimizing direct impacts of introduced brown trout requires actions that increase refuge habitat availability for vulnerable prey. Thus, habitat restoration activities should focus on creation and maintenance of off-channel habitats (backwaters and cutoff pools). Traditional stream restoration plans, designed to provide better habitat for large, predatory species (salmonids) may not provide sufficient refuge habitat required for the survival of vulnerable native species.

In summary, habitat occupied by southern leatherside chub and juvenile mountain sucker in streams in the eastern Great Basin is related to presence of brown trout. Adult and juvenile southern leatherside chub and juvenile mountain sucker exhibit nearly exclusive use of refugial backwater habitats when brown trout are present, compared to mostly main channel habitat use when brown trout are absent. Habitat alterations that reduce the availability of off-channel refuge habitats will likely exacerbate the potential negative effects of brown trout on native stream fishes.

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