

# Lethal and Nonlethal Effects of Predators on Stream Fish Species and Assemblages: A Synthesis of Predation Experiments

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*Abstract.*—Ecological communities are structured by a combination of stochastic and deterministic processes, the latter including both abiotic factors and biotic interactions such as predation. Many studies, mostly in relatively stable ecosystems such as lakes, have demonstrated top-down effects on community structure and function. Communities or species in dynamic nonequilibrium ecosystems such as streams may also respond strongly to predation pressure. In this chapter, we review experimental research on effects of predation on fish assemblages in lotic systems, focusing on developments in the decades since Matthews and Heins (1987). Direct experimental evidence indicates that predators strongly affect lotic fish assemblages via direct and indirect pathways of lethal and nonlethal interactions. Across studies, predators consistently reduced prey density, caused changes in prey habitat use, and decreased prey activity levels. Predators may also affect aspects of prey life history and reproduction in streams, and the presence of multiple predator species may result in prey risk enhancement. Our review identified five areas needing additional research that may lead to further advances in stream fish community ecology: (1) linking predation experiments with theoretical models of fish assemblage structure and function, (2) quantifying functional traits of predators and prey, (3) manipulating whole assemblages and testing multispecies interactions, (4) understanding the role of predation in human-modified ecosystems, and (5) application of analytical approaches that facilitate integration among these areas of research as well as with observational field studies.

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## Introduction

Ecological communities are structured by a combination of stochastic and deterministic processes, the latter including both abiotic factors and biotic interactions such as predation. Predators, simply defined as animals that kill and eat other animals, are a common feature of ecological communities and perform myriad functions through a combination of direct and indirect effects on prey species, their potential competitors, and resources. Direct and indirect effects of predators interact with abiotic drivers and may be spatially and temporally important in structuring various aspects of prey populations, communities, and ecosystem processes.

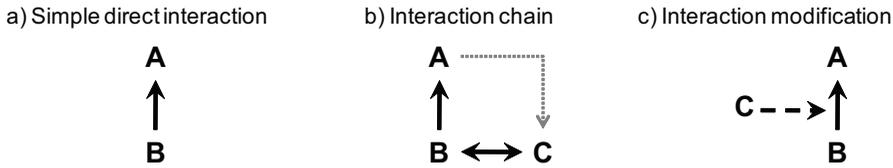
The simplest and most obvious effect of predators on their prey is through direct lethal (consumptive) interactions that affect prey abundance, size structure, and assemblage structure. However, predators may also affect prey through nonlethal (nonconsumptive) interactions, which result in changes in behavior, habitat and resource use, growth, and aspects of life history. Nonlethal interactions are easily overlooked, yet may enhance or obscure effects of lethal interactions, and effects of predator intimidation may greatly exceed consumption (Ripple and Beschta 2004; Preisser et al. 2005; Creel and Christianson 2008; Preisser and Bolnick 2008). Throughout this chapter, we refer to pairwise interactions between a predator and its prey or potential prey as either lethal or nonlethal direct interactions (Figure 1a).

Predators may exert indirect impacts on their prey or other food web components via density or trait-mediated interactions among two or more other species (Figure 1b–h). According to Abrams (1995), indirect interactions are those that require a change in some property of a (or many) “transmitter” species

for a change in the “initiator” species (e.g., density of a predatory species) to cause a change in the “receiving” species. Wootton (1993, 1994b) describes indirect interactions as either linked chains of direct interactions (interaction chains; Figure 1b) or changes in interactions between two species mediated by the presence of a third species (interaction modifications; Figure 1c). Although several slightly different definitions of indirect interactions exist (e.g., Miller and Kerfoot 1987; Strauss 1991; Billick and Case 1994; Wootton 1994b; Abrams 1995), of consensus across definitions is that indirect interactions require at least three participating species (or functional groups), in contrast to direct interactions that occur between species pairs. Trophic cascades, keystone predator effects, and exploitive competition are all examples of density-mediated indirect interactions, and trait-mediated indirect interactions are due to phenotypic changes in one of the interacting species (reviewed by Wootton 1994b; Werner and Peacor 2003). Indirect effects often result from a combination of lethal and nonlethal predator–prey interactions and may be comprised of both density- and trait-mediated effects (Werner and Peacor 2003; Peckarsky et al. 2008).

Natural communities typically have multiple predator species that often differ functionally, such as in body size and aspects of foraging mode. Rather than exhibiting independent linear effects, the presence of multiple predators may have nonlinear impacts on prey species (reviewed by Sih et al. 1998; Schmitz 2007). That is, the combined effect of multiple predators on a prey species is either less or greater than the expected effect given the simple combination of the independent predator effects. For example, the presence of multiple predator species may facilitate overall prey capture efficiency or result in lower prey capture efficiency through interference among predators (Figure

*Basic forms of direct and indirect interactions*



*Commonly investigated indirect interactions*

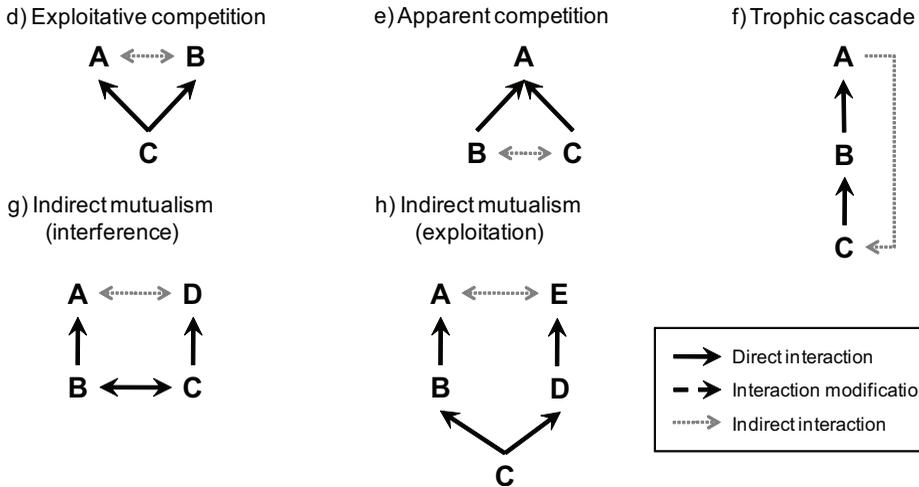


Figure 1. Basic forms of (a) direct and (b, c) indirect interactions, and (d–f) five commonly investigated indirect interactions. Letters represent species, solid arrows represent direct trophic interactions and direction of energy flow from resource to consumer, the dashed arrow indicates an interaction modification of one species on the direct interaction between two other species, and dotted arrows indicate direction of indirect interactions between species pairs in interaction chains. Interactions may be lethal (consumptive) or nonlethal (e.g., shifts in habitat use). Adapted from Figures 1 and 2 in Wootton (1994b).

2). From the prey’s standpoint, emergent multiple predator effects are either risk-enhancing or risk-reducing, and outcomes of multiple predator interactions may be predicted based on functional characteristics of predators and prey (e.g., habitat use and foraging mode; Schmitz 2007; Figure 2).

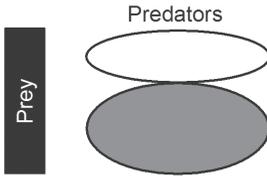
To date, the majority of research on predator–prey interactions has focused on relatively stable ecosystems such as lakes because biotic interactions are expected to more strongly affect communities in equilibrium systems where environmental conditions are comparatively benign (Krebs 2001). Lotic ecosystems

have received far less attention in this regard because the role of biotic interactions, including predation, is often assumed to be minimal in comparison with abiotic factors because of the dynamic (nonequilibrium) nature of these systems (reviewed in Matthews 1998; Jackson et al. 2001). Abiotic factors surely play an important role in organizing aquatic communities in lotic ecosystems, but it is likely that direct and indirect effects of predation interact with abiotic factors to affect stream fish communities at a variety of spatial and temporal scales (e.g., Gasith and Resh 1999; Power et al. 2008). Evidence of predation as contributing

*Predicting multiple predator effects*

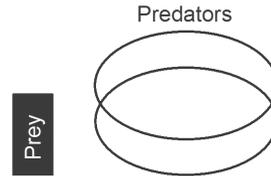
a) Substitutable

Broad prey habitat domain,  
complementary predator domains



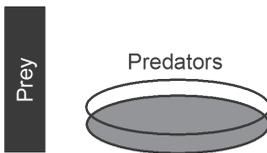
b) Risk enhancement

Narrow prey habitat domain,  
broad predator habitat domains



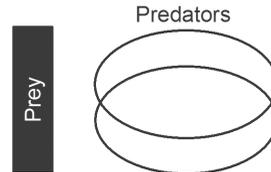
c) Risk reduction (intraguild predation)

Broad prey habitat domain,  
narrow predator habitat domain



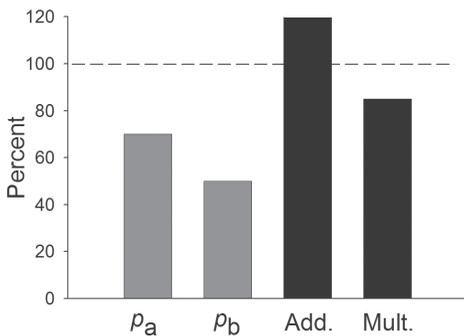
d) Risk reduction (interference)

Similarly narrow or broad prey  
and predator habitat domains

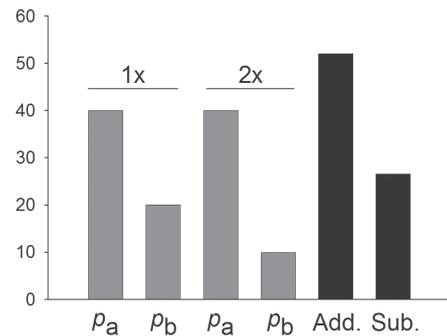


*Testing for multiple predator effects*

e) Model expectation



f) Experimental design



■ observed effect from single predator treatments ■ expected effect of both predators together

Figure 2. Predicting and testing for multiple predator effects. Predictions may be derived for multiple predator effects (a–d) based on aspects of prey and predator habitat use and predator foraging modes (adapted from Schmitz 2007). Range (narrow or broad) and overlap of habitat use is indicated by the relative height and position of the shapes representing prey (rectangle) and predators (ellipses). Shading of predator ellipses indicates similar or divergent foraging modes. Two different null models (e) and two experimental designs (f) have been used to test for multiple predator effects. Effects (e.g., percent mortality) of individual predators ( $P_a$ ,  $P_b$ ) on a shared prey species are represented by gray bars, and black bars represent the expected effect of both predators together based on (e) the additive (Add.) or multiplicative (Mult.) models, and (f) the additive (Add.) or substitutive (Sub.) experimental designs using the multiplicative model. 1× and 2× indicate the density level. Note that the additive null model can yield an expected effect that exceeds 100%, a problem that is corrected in the multiplicative model.

to observed spatiotemporal patterns in fish assemblage structure, habitat use, distribution, and life history is common in observational studies (e.g., Fraser and Sise 1980; Reznick and Endler 1982; Power 1984; Gilliam et al. 1993; Fraser et al. 1995; Rodríguez and Lewis 1997; Fraser et al. 2001; Magalhães et al. 2002; Layman et al. 2005; Hoeinghaus et al. 2007; Reyjol et al. 2008; Walsh and Reznick 2008; Pelicice and Agostinho 2009), and many studies have experimentally demonstrated strong effects of predation on invertebrate and vertebrate assemblages across a diversity of lotic systems (e.g., Stein and Magnuson 1976; Petranka 1983; Flecker and Allan 1984; Power et al. 1992; Nystrom and McIntosh 2003; Fairchild and Holomuzki 2005).

Matthews (1998) noted that of the 30 contributions in *Community and Evolutionary Ecology of North American Stream Fishes* (Matthews and Heins 1987), only the papers by Fraser et al. (1987) and Schlosser (1987a) addressed the role of predator–prey interactions on stream fish assemblages. In this chapter, we review experimental research on effects of predation on fish species and assemblages in lotic systems, focusing on developments in the decades since Matthews and Heins (1987). Several generalities may be gleaned from these studies, yet our review also identifies many areas needing additional research that may lead to further advances in stream fish community ecology.

## Review of Experimental Research

### *Scope and Limitations*

Predator–prey interactions are inherently local in scale, but resulting direct and indirect effects of predation may cascade across larger spatial and temporal scales. Because the majority of previous experimental research was conducted at small scales (e.g., riffle-pool segments), our review retains this bias for no better reason than

the paucity of studies at larger scales in lotic systems. Although effects of predators on prey fishes may have important indirect effects on other species of the fish assemblage and other food web compartments, our review focuses on lethal and nonlethal direct interactions of predators on lotic fish assemblages or species because studies explicitly testing or quantifying indirect interactions within lotic fish assemblages are lacking (but see Harvey 1991; Blanchet et al. 2008). Previous research demonstrating trophic cascades in lotic systems is a notable exception (e.g., Power et al. 1985; Power 1990; Flecker and Townsend 1994; Forrester et al. 1999; Gelwick 2000; Woodward et al. 2008); however, as our focus is on lotic fish assemblages and not lotic ecosystems, we do not review the trophic cascade literature herein. We did not endeavor to review stream fish responses to chemical cues from predators (kairomones) or alarm cues from injured prey at this time, but refer the reader to reviews by Chivers and Smith (1998) and Brown (2003) and studies by Blanchet et al. (2007), Scheurer et al. (2007), and Sunardi et al. (2007a) for some recent examples. Similarly beyond the scope of this review were prey learning and effects of acquired predator recognition on the outcome of predator–prey interactions (e.g., Mathis et al. 1996; Brown and Godin 1999; Haberli et al. 2005).

### *General Overview*

Given the aforementioned scope of our review, the following sections are based on 43 studies (Table 1) identified via database searches and cited reference searches. Table 1 is a representative compilation of experimental research directly manipulating predator–prey fish interactions in lotic systems or on lotic fish species in stream mesocosms over the past three decades. Experimental duration ranged from several days (most studies) to as long as several

Table 1. Summary of experimental studies of predator-prey interactions in lotic fish assemblages.

Reference	Latitude <sup>a</sup>	Venue <sup>b</sup>	Environ <sup>c</sup>	Prey response		Predator treatment			
				Type <sup>d</sup>	N species <sup>e</sup>	Taxa	N species <sup>e</sup>	Type <sup>f</sup>	Emergent <sup>g</sup>
Fraser and Cerri 1982	Temp	M	HC	HU, DL	2 (indiv)	Fish	1	P/A	-
Cerri and Fraser 1983	Temp	M	RD	HU	1	Fish	1	P/A	-
Power et al. 1985	Temp	F	-	MO, SI, HU, RU, FR, MV	1	Fish	1	P/A	-
Gilliam and Fraser 1987	Temp	M	RD	MO, RU, FR	1	Fish	1	DN	-
Fraser et al. 1987	Temp	F+M	HC, RD	MO, SI, HU, RU, FR, DL	1	Fish	1	P/A	-
Reznick and Bryga 1987	Trop	F	-	SI, LH	1	Fish	1	P/A	-
Rahel and Stein 1988	Temp	M	-	MO, RU, AR	1	Fish, invert	2 (both)	P/A	N
Schlosser 1987b	Temp	M	HC	MO, SI, HU, RU	3 (indiv)	Fish	1	P/A	-
Schlosser 1988a	Temp	M	HC	MO, HU, RU	1	Fish	2 (indiv)	P/A	N
Schlosser 1988b	Temp	M	HC	MO, SI, HU, RU, DL	1	Fish	1	P/A	-
Schlosser and Ebel 1989	Temp	F+M	HC	MO, SI, HU, RU	3 (indiv)	Fish	1	P/A	-
Reznick et al. 1990	Trop	F	-	SI, LH	1	Fish	1	P/A	-
Harvey 1991	Temp	F	FL	MO, DN, SI, RU, OT	5+ (comb)	Fish	1	P/A, DN	-
Harvey and Stewart 1991	Temp	F	HC, FL	MO, SI	3 (indiv)	Bird, mammal	2+(comb)	AM	N
Angermeier 1992	Temp	M	HC, FL	MO, SI, RU, AR, DL	3 (indiv)	Fish	1	P/A, DN	-
Fraser and Gilliam 1992	Trop	F+M	-	MO, SI, HU, RU, MV, GR	2 (both)	Fish	1+	P/A, DN	N
Greenberg 1994	Temp	M	FL	LH, DL	1	Fish	1	P/A	-
Brown and Brasher 1995	Temp	M	-	SI, HU, RU	2 (both)	Fish	1	P/A	-
Fraser et al. 1995	Trop	F+M	-	MO, HU, DS, MV	1	Fish	1	P/A	-
Grossman et al. 1995	Temp	M	TM	RU, DL	1	Fish	1	P/A	-
Lohr and Fausch 1996	Temp	M	-	MO, HU, RU	1	Fish	1	P/A	-
Greenberg 1999	Temp	M	FL	MO, HU, RU	2 (both)	Fish	1	P/A	-
Allouche and Gaudin 2001	Temp	M	HC, FL	HU, RU, FR, GR	1	Bird	1	P/A	-

Table 1. Continued.

Reference	Latitude <sup>a</sup>	Venue <sup>b</sup>	Environ <sup>c</sup>	Prey response		Predator treatment			
				Type <sup>d</sup>	N species <sup>e</sup>	Taxa	N species <sup>e</sup>	Type <sup>f</sup>	Emergent <sup>g</sup>
Gilliam and Fraser 2001	Trop	F+M	HC, FL	SI, MV, SE	1	Fish	1	P/A	-
Reinhardt et al. 2001	Temp	F	-	MO, SI, GR	1	Fish	1	P/A	-
Schaefer 2001	Temp	M	FL, OT	MV	3 (both)	Fish	1	P/A	-
White and Harvey 2001	Temp	F	HC	MO	1	Fish	1+	P/A	-
Bryan et al. 2002	Temp	M	-	MO, RU, AR	1	Fish, invert	2+ (both)	P/A	Y
Skalski and Gilliam 2002	Temp	M	RD	MO, FR, GR	1	Fish	1	DN	-
Glova 2003	Temp	M	-	MO, HU	1	Fish	1	P/A	-
Steinmetz et al. 2003	Temp	F	-	DN, SI	5+ (comb)	Bird	2 (comb)	DN	N
Fraser et al. 2004	Trop	F+M	-	RU, FR, GR, DL, OT	1	Fish	1	P/A	-
Harvey et al. 2004	Temp	M	HC	MO, RU, AR	1	Fish	2+ (both)	P/A	Y
Layman and Winemiller 2004	Trop	F	-	DN, SI, DL	50+ (comb)	Fish	7 (comb)	P/A	N
Magoulick 2004	Temp	F	-	DN, SI, RU	4+ (comb)	Fish	1	P/A	-
Greenberg et al. 2005	Temp	F	-	GR, OT	1	Fish	1	P/A	-
Knight and Gido 2005	Temp	M	HC	MO, HU, RU	4 (both)	Fish	1	P/A	-
Nilsson and Persson 2005	Temp	F	-	GR	1	Fish	1	P/A	-
Fraser et al. 2006	Trop	F	-	SI, MV, DL	1	Fish	1	P/A	N
Nannini and Belk 2006	Temp	F+M	-	MO, HU, RU, AR, OT	2 (both)	Fish	2 (both)	P/A	-
Sunardi et al. 2007b	Temp	M	-	HU, FR, AR, GR, DL, OT	1	Fish	1	P/A	-
Blanchet et al. 2008	Temp	F	FL	AR, GR, DL	1	Fish	1	P/A	-
Steinmetz et al. 2008	Temp	F	-	MO, SI	2 (comb)	Fish, bird	2+ (both)	P/A	Y

<sup>a</sup> Latitude: Temp = temperate, Trop = tropical.

<sup>b</sup> Venue: F = field, M = mesocosm, F+M = both field and mesocosm components.

<sup>c</sup> Environmental treatments: HC = habitat complexity/cover, FL = water flow/volume, RD = resource density, TM = temperature, OT = other.

<sup>d</sup> Response: MO = mortality, DN = density, SI = size structure or comparison, HU = habitat use (macro), RU = refuge use (micro; including depth), DS = dispersal (landscape), MV = movement (macro), FR = foraging rate/time, AR = activity rate, GR = growth, LH = life-history traits/reproduction, DL = diel comparison, SE = seasonal/temporal, OT = other (e.g., courtship, escape response).

<sup>e</sup> Number of species: comb = combined, indiv = individually, both = combined and individually.

<sup>f</sup> Type of predator treatment: DN = density, P/A = presence vs. absence (including exclusion experiments), AM = ambient (environment manipulated).

<sup>g</sup> Emergent impacts of multiple predators tested?: Y = yes, N = no.



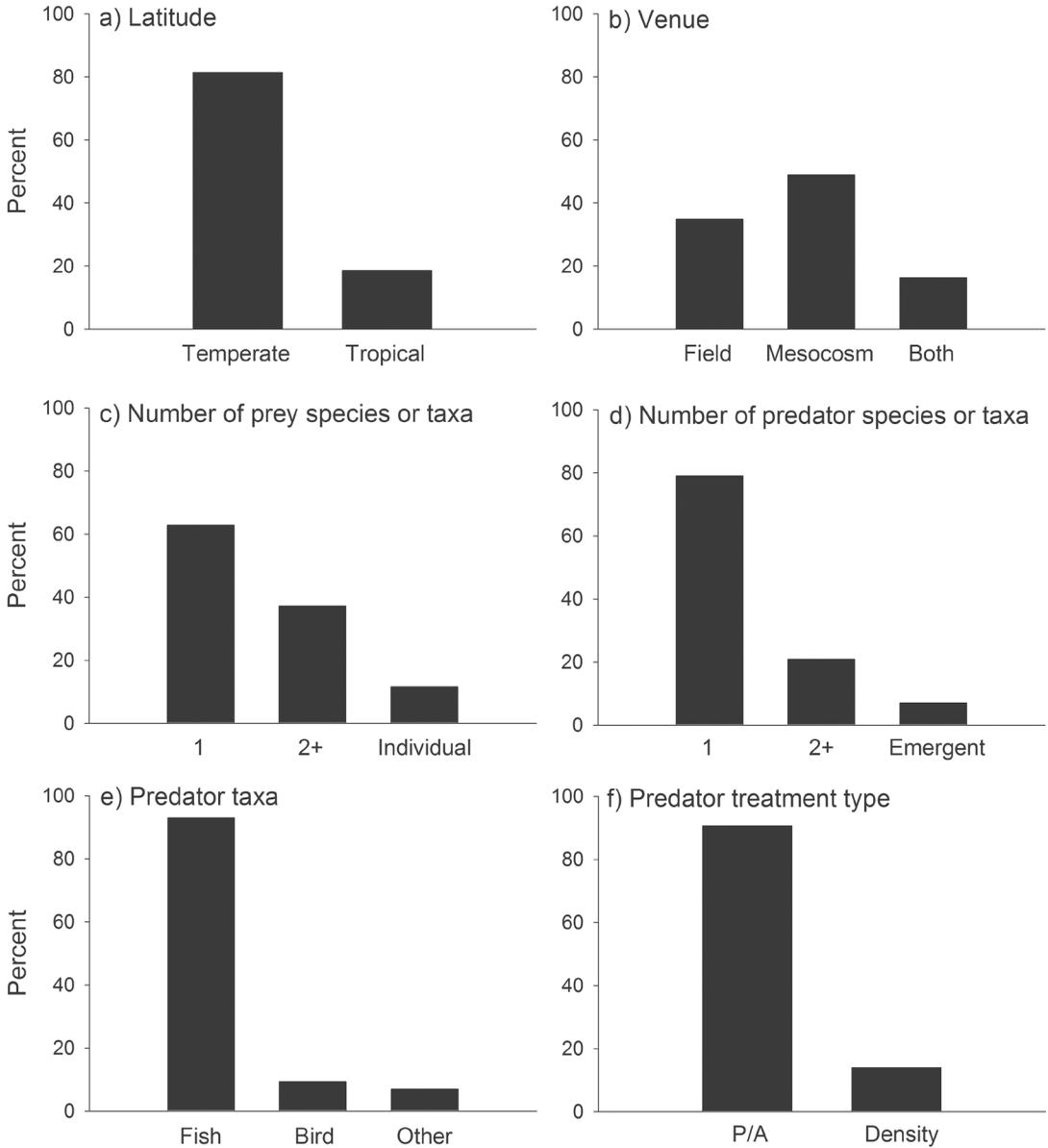


Figure 4. Classification of predator–prey experiments in lotic fish assemblages according to (a) latitude, (b) experimental venue, (c) number of prey species or taxa examined, (d) number of predator species or taxa included, (e) predator taxa used, and (f) type of predator treatment (P/A = presence/absence). Total percent across groups may slightly exceed 100% as several studies included multiple experiments that differed in design. For experiments with two or more prey species (designated as 2+), those that manipulated predator–prey interactions on an individual species basis are shown in addition to the total. For predator treatments with two or more species (designated as 2+), those studies that explicitly tested for emergent impacts of multiple predators are shown in addition to the total.

We identified 14 broad classes of response variables measured across studies (Table 1), which differed greatly in their frequency of in-

vestigation (Figure 5). Most studies measured multiple response variables, and 30 of the 42 studies measured three or more of our broad

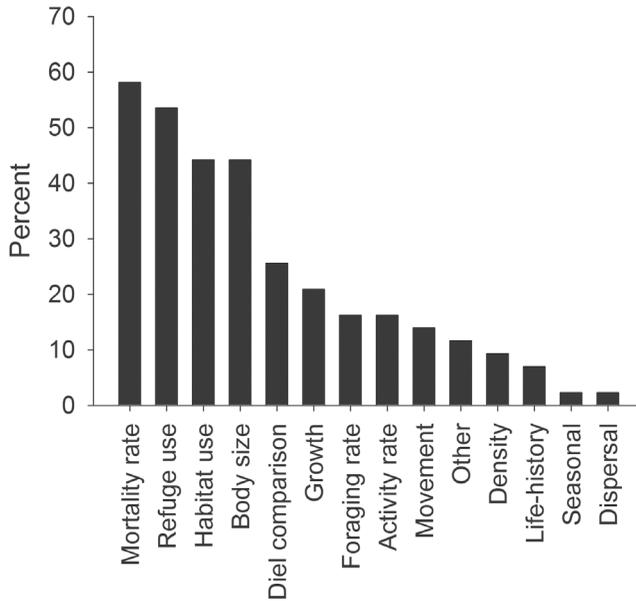


Figure 5. Percent of studies that measured each prey response category. The total across response categories exceeds 100% because most studies measured multiple response variables (Table 1).

response classes (Table 1). Mortality, micro-habitat/refuge use, macrohabitat use, and size-structure or body-size contrasts were the most frequently employed response variables, with each measured in 44–58% of all studies (Figure 5). Approximately 26% of all studies examined diel variation in response variables. Growth rates were measured in nine studies, and eight or fewer studies examined effects of predators on prey foraging rates, activity rates, and life history attributes, among other factors.

#### *Mortality and Density*

Perhaps the most obvious and easiest to measure effect of predators on their prey is through direct lethal interactions, namely consumption. Fittingly, the most frequently examined response variable in the experimental studies reviewed, along with refuge use, was mortality rate (Figure 5; Table 1). Effects of predators on prey fish density were only examined in about 9% of the studies; however, the limited use of this comparable response variable is related to

aspects of experimental design (i.e., field enclosure of predators in natural prey assemblages versus stocking of prey fish into experimental treatments). Across studies measuring prey fish mortality rates or density, the presence of predators significantly reduced prey populations compared to no-predator controls, increased prey fish density in predator exclusion experiments, or decreased prey density in predator addition treatments in field settings. Significant variation in the effectiveness of predators to reduce prey populations was mediated by predator and prey identities and body size, habitat depth and complexity, and predator density.

Studies demonstrating variation in predation rates as a function of predator or prey identity and body size are common. Schlosser (1987b) found mortality rates of juvenile smallmouth bass *Micropterus dolomieu*, hornyhead chub *Nocomis biguttatus*, and white sucker *Catostomus commersonii* to differ among species by as much as 10 individuals

per 48 h in the presence of a single adult smallmouth bass. In the same experimental system, Schlosser (1988a) found that mortality rates of brassy minnow *Hybognathus hankinsoni* differed greatly between treatments with adult creek chub *Semotilus atromaculatus* or smallmouth bass (the more successful predator), and that mortality rates of small hornyhead chub (60–65 mm) were more than three times higher than large hornyhead chub (100–110 mm) in the presence of adult smallmouth bass (Schlosser 1988b). Similarly, Magoulick (2004) observed a size-based shift in prey densities in response to the addition of largemouth bass *Micropterus salmoides* to stream pools, with smaller size-classes exhibiting the greatest changes in densities. Even prey species with similar morphologies and ecologies may respond differently to predation threat, resulting in different mortality rates (Nannini and Belk 2006). Like the above studies on temperate assemblages, Fraser and Gilliam (1992) observed lower mortality of comparatively larger guppies *Poecilia reticulata* than giant rivulus (also known as killifish) *Rivulus hartii* in the presence of predatory trahira *Hoplias malabaricus* in tropical streams of Trinidad. Also in the tropics, but conducted in a much more species-rich lowland river, Layman and Wine-miller (2004) found that exclusion of a guild of large-bodied piscivores from sandbank habitats resulted in an approximately 250% daytime increase in the density of medium-sized prey fishes, corresponding with the size-class of prey most often found in stomach contents of large piscivores. The only other study from a species-rich tropical floodplain river, A. C. Petry and colleagues (Universidade Estadual de Maringá, Brasil, unpublished manuscript) manipulated predator density in entire floodplain lagoons of the upper Paraná River, Brazil and examined effects on prey fish abundance (density), species richness, and evenness. In

contrast, exclusion of piscivorous birds, great blue herons *Ardea herodias* and belted kingfishers *Ceryle alcyon*, resulted in higher densities of larger central stonerollers *Campostoma anomalum* and striped shiners *Luxilus chrysocephalus* in prairie streams (Steinmetz et al. 2003).

The ability of predators to reduce prey populations also may vary in relation to the availability of instream cover, water depth, or current velocity, but the importance of these environmental variables in mediating predator–prey interactions appears to be dependent on the identities of the predator and prey species. For example, Harvey and Stewart (1991) found mortality rates of central stonerollers in stream pools frequented by green-backed herons *Butorides striatus* and raccoons *Procyon lotor* to be mediated by water depth and the availability of shelter. Survivorship was four times greater in deep pools (40 cm) versus shallow pools (10 cm) without shelter and comparable among deep pools and shallow pools with shelter. Similar to a conceptual model by Power (1987), Harvey and Stewart (1991) suggested that larger prey fish are at greater predation risk from terrestrial predators such as wading birds and mammals in shallow water, whereas smaller prey fish are at greater predation risk from piscivorous fish in deeper water. White and Harvey (2001) found mortality of prickly sculpin *Cottus asper* from predation by Sacramento pikeminnow *Ptychocheilus grandis* to be much higher in pools than in riffles and greatly reduced when artificial cover was provided. Angermeier (1992) found predation rates of adult rock bass *Ambloplites rupestris* on fantail darters *Etheostoma flabellare* and central stonerollers to increase with depth, whereas predation rates on pumpkinseeds *Lepomis gibbosus* did not differ with water depth. In this case, the presence of cover in the experimental stream did not significantly affect predation rates for any species. Similarly,

Harvey et al. (2004) found no effect of a 10-fold increase in cover availability on predation rates of Sacramento pikeminnow and sculpin (prickly sculpin and coastrange sculpin *C. aleuticus*) on speckled dace *Rhinichthys osculus*. Predation rates of northern pike *Esox lucius* on brown trout *Salmo trutta* or grayling *Thymallus thymallus* did not differ between high and low discharge treatments in experimental stream studies by Greenberg (1994, 1999).

Higher densities of predators may be expected to result in higher overall prey mortality but lower per capita predation rates due to interference among predators. Unfortunately, only a handful of studies manipulated predator density rather than simply presence or absence, and almost half of those studies measured response variables other than prey mortality or density in response to different predator densities (i.e., Angermeier 1992; Fraser and Gilliam 1992). As part of a larger study evaluating effects of resource density on risk taking by prey fishes, Gilliam and Fraser (1987) estimated mortality rates of juvenile creek chubs in the presence of different densities of adult creek chub and found a positive linear relationship between predator density and prey mortality rates. Harvey (1991) observed size-based responses of the fish assemblage to variation in density of largemouth bass in stream pools. Minnows and juvenile sunfishes less than 80 mm exhibited strong declines in abundance with increasing bass density, whereas abundance of adult sunfish increased slightly with increasing bass density. In addition to excluding avian predators, Steinmetz et al. (2003) also measured fish density and body size in response to ambient and increased levels of predation. Contrary to the strong response of some species to exclusion of avian predators, no difference in prey fish density or size structure was observed between ambient and increased levels of avian predation.

### Macrohabitat, Microhabitat, and Refuge Use

In addition to the lethal effects of predators on prey species discussed above, predation risk may result in nonlethal (or nonconsumptive) effects such as shifts in habitat use and foraging activity. Along with mortality rates, the most frequently measured response variables in predator-prey experiments in lotic systems are prey micro- and macrohabitat use, including use of refuges from predation provided by shallow margins or instream cover (Figure 5). The presence of piscivorous fish consistently resulted in shifts by prey species or size-classes into shallower microhabitats within a macrohabitat (e.g., pool) or shifts from pools to connected shallow-water macrohabitats (e.g., riffles). However, use of instream cover appears to differ among predator-prey combinations (e.g., Rahel and Stein 1988; Schlosser 1988a; Bryan et al. 2002; Knight and Gido 2005) and environmental context, such as if preferred shallow water refugia are available (e.g., Allouche and Gaudin 2001). Studies have found increases, decreases, and no change in the use of structurally complex habitats designed as cover in experimental treatments with and without predators (e.g., Angermeier 1992; Grossman et al. 1995; White and Harvey 2001), and instream cover may not necessarily function as a refuge from predation (e.g., Harvey et al. 2004).

Predation threat from piscivorous fish consistently resulted in increased use of shallow-water micro- and macrohabitats of prey species across studies. Within pool macrohabitats, several studies observed prey species to preferentially utilize deeper water in the absence of a predator, but shift to shallow margins when a predator is present (e.g., Power et al. 1985; Harvey 1991; Fraser and Gilliam 1992; Fraser et al. 2004; Magoulick 2004). For example, in a stream pool of Brier Creek, Oklahoma, Harvey (1991) observed bigeye shiners *Notropis boops*,

central stonerollers and juveniles of green sunfish *Lepomis cyanellus* and longear sunfish *L. megalotis* to shift from deeper water to shallower margins following the introduction of largemouth bass, whereas adult sunfishes that exceeded gape limitations of the predator did not alter their depth distributions. Higher predator densities resulted in a more pronounced shift in depth distributions of vulnerable prey species. Similarly, Fraser and Gilliam (1992) observed shifts in within-pool habitat use, mediated by prey body size and diurnal period, in tropical stream pools in the presence of a nocturnal predator, trahira. Comparatively larger giant rivulus did not exhibit significant shifts in its depth distribution in the presence of trahira, whereas both small and large size-classes of guppy (both of which are smaller than giant rivulus) shifted to shallow pool margins during the crepuscular period as activity of the nocturnal predator increases.

When pools are connected with shallower riffles and runs, experimental studies often find the presence of piscivorous fish to result in macrohabitat shifts by prey fish from pools (typically preferred habitats in the absence of the predator) to riffles and runs, depending on aspects of prey body size and the predator species (e.g., Schlosser 1987b, 1988a, 1988b; Schlosser and Ebel 1989; Greenberg 1994, 1999; Brown and Brasher 1995). In a series of experiments by Schlosser (1987b, 1988a, 1988b) and Schlosser and Ebel (1989), the strength of macrohabitat shifts differed among prey species for a given predator as well as for different predator-prey combinations. For example, smallmouth bass are more efficient predators of brassy minnows than are creek chub, and the degree of macrohabitat shifts among predator treatments corresponds with the relative risk from predation (Schlosser 1988a). Similarly, prey species may respond to predation threat from the same predator in a

different manner due to differences in their relative risk of predation (Schlosser 1987b). Macrohabitat shifts may be comparable among size classes of the same species, even when predation rates differ among size-classes, if a threshold level of predation risk has been exceeded (Schlosser 1988b). However, some prey species may not shift from deep to shallow-water macrohabitats even when predation rates are high, as observed by Schlosser and Ebel (1989) for northern redbelly dace *Phoxinus eos* under predation threat from creek chub.

#### *Prey Activity, Foraging Rates, and Growth*

Comparatively active prey may more frequently encounter predators or draw more attention from predators than sedentary prey, potentially resulting in higher mortality. However, more active foragers may acquire more resources than less active or refuging individuals, which may lead to a trade-off between resource acquisition (with potentially cascading effects on growth, reproduction, and population dynamics) and predation risk when predators are present (Brown and Kotler 2004). Only 16–21% of the studies in Table 1 measured effects of predators on activity rates (nonforaging), foraging rates, or growth of prey fishes (Figure 5).

Gilliam and Fraser (1987) conducted a mesocosm experiment to test prey (juvenile creek chub) choice of habitats differing in resource availability (*Tubifex* spp. worms) and predation risk (different densities of adult creek chub). They predicted that prey should choose habitats in a manner that minimizes the ratio of mortality ( $\mu$ ) to foraging rate ( $f$ ). Based on independent measures of mortality rates with different predator densities and foraging rates in relation to different resource densities, Gilliam and Fraser (1987) found that juvenile creek chub chose habitats in the manner predicted by the “minimize  $\mu/f$  rule.” Their

findings suggest that prey may not simply optimally forage to maximize energetic gain per time spent foraging, but also choose habitats to minimize predation risk relative to energy gain. Modifications of the “minimize  $\mu/f$  rule” can account for different metabolic costs of habitats (e.g., due to differences in water velocity or temperature) or the lack of a true refuge from predation (Gilliam and Fraser 1987).

Skalski and Gilliam (2002) conducted the only other study examining prey activity or growth rates that contrasted multiple resource and predator density levels. They examined mortality, foraging behavior and resulting growth of bluehead chubs *Nocomis leptoccephalus* in an experimental setting with variable resource densities and predation threat (green sunfish *Lepomis cyanellus*). Similar to findings from Gilliam and Fraser (1987), Skalski and Gilliam (2002) found that bluehead chubs adjusted their foraging rate under predation threat to minimize the ratio of mortality to growth. Furthermore, their models indicated that age (rather than body size alone) was an important factor determining prey behavioral responses to resource and predation gradients. Younger, smaller bluehead chubs placed more value on growth in comparison with mortality than older, larger bluehead chubs with higher reproductive potential (Skalski and Gilliam 2002).

Fraser et al. (1987) examined prey foraging rate in response to different resource densities in the presence or absence of a model predator and found that foraging rate increased with resource density but was depressed at all resource levels by the presence of a predator. Similarly, all other studies examining activity rates or foraging rates in the presence or absence of a predator under constant resources observed significant decreases in activity or foraging rates and increased use of cover when available (Angermeier 1992; Allouche and Gaudin 2001; Bryan et al. 2002; Fraser et al. 2004; Nannini and Belk 2006; Su-

nard et al. 2007b; Blanchet et al. 2008). For example, although guppies are often considered diurnal, Fraser et al. (2004) observed increased foraging rates at night when released from predation pressure of a nocturnal predator. When exposed to predation threat by avian predators, juvenile European chub *Squalius cephalus* greatly reduced foraging rates and increased use of overhead cover (Allouche and Gaudin 2001).

Predator-induced changes in foraging behavior may affect prey growth rates. Fraser et al. (2004) found nocturnal foraging of guppies to be as profitable as diurnal foraging, and that inhibition of foraging by a nocturnal predator results in a substantial growth penalty. Similarly, decreased foraging by juvenile European chub under avian predation risk translated to slower growth rates than in the absence of predators (Allouche and Gaudin 2001). Sunardi et al. (2007b) found that decreased growth of a Japanese minnow, stone moroko *Pseudorasbora parva*, due to reduced foraging under predation threat was exacerbated by increased metabolic demands of swimming in a higher velocity riffle macrohabitat used in the presence of the predator. Unlike the previous studies, Blanchet et al. (2008) did not find a significant effect of predator-induced decrease in foraging activity on growth rates, which they attributed to a dominant effect of water velocity and elevated levels of resource availability on growth rates of juvenile Atlantic salmon *Salmo salar*. Other studies found decreased growth rates of prey species when in the presence of a predator (Table 1) but did not directly link the slower growth rates to predator-induced decreases in foraging activity or energy expenditure as in the above studies.

#### *Emergent Impacts of Multiple Predators*

Only four studies in our review used experimental designs that allowed for testing emer-

gent impacts of multiple predators on fishes in lotic systems (Rahel and Stein 1988; Bryan et al. 2002; Harvey et al. 2004; Steinmetz et al. 2008). All four studies measured response variables as a function of two predators independently and combined using an additive experimental design. Rahel and Stein (1988) did not explicitly test for emergent impacts; however, the latter studies all tested the null expectation of multiple predator effects based on the multiplicative model. Rahel and Stein (1988) observed higher activity rates and lower refuge use of johnny darters *Etheostoma nigrum* in the presence of both smallmouth bass and rusty crayfish *Oreoctes rusticus* than in the presence of smallmouth bass alone. Both Harvey et al. (2004) and Steinmetz et al. (2008) found significant emergent impacts of multiple predators on prey mortality rates, with prey suffering risk enhancement (greater mortality than expected) when both predators were present. As may be predicted for risk enhancement to occur (Sih et al. 1998), the two predators differed in their microhabitat use and foraging modes in both studies and were both effective predators in independent trials. In Harvey et al. (2004), the Sacramento pikeminnow is a pelagic predator, whereas sculpin frequently occurred and foraged within the available in-stream cover. Speckled dace avoided cover in the presence of sculpin, thereby facilitating predation by pikeminnow (Harvey et al. 2004). Risk enhancement of striped shiners and central stonerollers in the presence of smallmouth bass and herons was primarily driven by the smallest size-class (<70 mm), which apparently were forced from shallow water into deeper water to avoid the avian predator and were then consumed by bass (Steinmetz et al. 2008). Similarly, the combined presence of nonnative crayfish (northern crayfish *O. virilis*) and rainbow trout *Oncorhynchus mykiss* resulted in a significant emergent impact on refuge use and

activity rates (potentially enhancing predation risk) by Little Colorado spinedace *Lepidomeda vittata* (Bryan et al. 2002).

#### *Predator-Induced Variation in Life History and Reproduction*

Although several comparative studies relate life history variation and evolution of freshwater fishes to predation (e.g., Reznick and Endler 1982; Johnson and Belk 1999; Johnson and Belk 2001; Carlson et al. 2007; Langerhans et al. 2007), we are aware of only three studies, all from streams in Trinidad, that experimentally examined effects of predation on aspects of fish life history or reproduction in lotic systems (Table 1). Similar to Reznick and Bryga (1987), Reznick et al. (1990) introduced guppies from a population that contained pike cichlid *Crenicichla alta*, a predator of large sexually mature size-classes of guppy, into a tributary lacking guppies but containing rivulus, a predator of small immature-size classes, thereby changing the selective pressures on guppies exerted by size-dependent predation. Reznick et al. (1990) tracked life history phenotypes of the two guppy populations over 11 years (30–60 generations) and found significant shifts in life history attributes as expected based on life history theory. Relative to the control stream with pike cichlid, guppies in the presence of giant rivulus matured at a later age and larger size and produced fewer but larger offspring. Fraser and Gilliam (1992) found predation threat by trahira to suppress total egg production of killifish by approximately 50% and that giant rivulus modified reproductive behavior in the presence of the predator, resulting in spatial patchiness of egg deposition and pulsed patterns of production. Although they did not measure reproductive effort or aspects of life history, Fraser et al. (2004) found that daytime courtship activity in guppies was reduced by the presence of a nocturnal predator (trahira)

through its negative effect on nocturnal foraging time and growth. Reduced courtship activity and growth may affect reproductive traits.

### *Movement and Dispersal*

Most studies of predator–prey interactions in lotic systems are conducted at scales too small to examine influences of predation pressure on patterns of movement or dispersal across stream reach or landscape scales. Power et al. (1985) and Fraser and Gilliam (1992) examined prey emigration rates from a predator invasion pool to pools located just upstream or downstream. In both studies, net prey emigration rates to adjacent stream reaches in response to predation threat were high (approaching 50% in some cases) and consistently exceeded predation rates. Mortality and emigration rates were affected by body size and appear dependent on the preferred prey size of the predator present. Similarly, Schaefer (2001) found interpool movement of three small cyprinids from pools with a caged predator to be almost three times that of the background (no predator present) rate. Fraser et al. (1995) and Gilliam and Fraser (2001) created a unique field mesocosm assembly consisting of multiple experimental tributaries connected to a shared stream channel that was an actual third-order stream to examine effects of predators on prey movement among tributaries and main-stem reaches. In a first experiment, Fraser et al. (1995) found that the presence of a predator in the main-stem section below a tributary caused a significant shift in the density of giant rivulus from the main stem into the connected tributary (a refuge from predation) due to a combination of lethal and nonlethal effects. When tributary pairs were connected by a stretch of main-stem stream with or without trahira, the predator functioned as a barrier to dispersal from tributaries into the main stem through predation (high mortality of giant rivulus entering the

main stem). At the same time, predation risk also facilitated among tributary dispersal as the few giant rivulus surviving after entering the main stem in the presence of a predator ascended the adjacent tributary, whereas giant rivulus tended to remain in the main stem in the absence of a predator (Fraser et al. 1995). Subsequent experiments (Gilliam and Fraser 2001) examined the effect of physical structure in the littoral zone of the main-stem stream on longitudinal and tributary-to-tributary movement of giant rivulus in the presence of trahira. Instream cover facilitated both longitudinal movement along the main stem and colonization of upstream tributaries in the presence of a predator. Combined with field observations and a mark–recapture study in natural stream reaches with and without predatory fish, these findings demonstrate that predators can fragment populations through avoidance of high-risk habitats, but also increase movement of survivors into safer habitats, with the probability of emigration and dispersal dependent on body size and affected by habitat characteristics (Fraser et al. 1995, 2006; Gilliam and Fraser 2001).

### *Temporal Variation*

Aspects of predator sensory capability (e.g., visual versus nonvisual predator) may interact with environmental conditions to differently affect their prey (e.g., Rodríguez and Lewis 1997), including the time of day that predation effects occur. Several predation experiments measured response variables at multiple times during the diel period (primarily once each during the day and at night; Table 1; Figure 5). Prey response to predation often differs along the diurnal cycle, with the direction and magnitude of the response dependent on characteristics of the predator and prey (e.g., diurnal versus nocturnal predator, body size). For example, Fraser and Cerri (1982) observed dif-

ferent patterns of prey macrohabitat use during day and night in the presence of a predator, and Fraser and Gilliam (1992) observed diurnal shifts in microhabitat use of prey under predation threat. As discussed above, guppy nocturnal foraging rates were depressed when a nocturnal predator was present, affecting growth and courtship activity (Fraser et al. 2004). Similarly, Blanchet et al. (2008) found lower activity of prey during the day but not at night in the presence of a diurnal predator. The only long-term study we found that was able to adequately address seasonal variation in prey response to predation was conducted in tropical streams by Gilliam and Fraser (2001). They found that prey dispersal distance was greater almost year-round in the presence of predators, and unlike streams lacking predators, distance dispersed was significantly correlated with body size and tied to hydrological seasonality that increased habitat connectivity and facilitated dispersal.

### Summary of Previous Studies and Considerations for Future Research

Along with comparative and observational studies, direct experimental evidence indicates that predators may strongly affect lotic fish assemblages, their resources, and competitors via direct and indirect pathways of lethal and nonlethal interactions. Three primary trends in response of lotic fish assemblages to predation pressure were evident in our review and are comparable with trends from lentic systems (Matthews 1998; Jackson et al. 2001). First, predators generally reduced prey density (or increased prey density in predator exclusion experiments), and predator effectiveness was mediated by predator and prey identities and body size, habitat depth and complexity, and predator functional diversity and density. Second, prey fish moved to shallower margins within a given macrohabitat or to connected

shallow macrohabitats such as riffles in the presence of piscivorous fish, and in the opposite direction to avoid predation by terrestrial predators. Shifts in micro- and macrohabitat use were mediated by prey body size and predator efficacy. Third, in addition to modifying habitat use, overall prey activity and foraging levels were consistently depressed in the presence of predators, resulting in slower growth rates. In addition to these three main patterns, evidence also indicates that size-based predation pressure may result in life history shifts in prey species to maximize fitness, predator-induced emigration of prey fish from a nonisolated macrohabitat likely exceeds mortality from predation, and the presence of multiple predators may result in risk enhancement of prey species when the predators differ functionally in foraging mode. In addition to the trends noted above, some aspects of predator-prey interactions appear to be context and species specific. For example, diel variation in prey responses to predation and the use of instream cover and its value as a refuge differed among studies and species combinations.

Several changes in experimental studies of predator-prey interactions in lotic systems have taken place since the publication of Matthews (1998). Perhaps most obvious is the far greater diversity of species used in predation studies during the past decade. Matthews (1998) noted that most studies used largemouth bass, smallmouth bass, or creek chub as predators and an equally small suite of minnows as prey. As evidenced in the above sections, a much greater diversity of predator-prey combinations are being used in more recent experimental studies, a trend that appears to have been facilitated by experiments directed at applied issues such as effects of invasive piscivores on native species (e.g., White and Harvey 2001; Bryan et al. 2002; Harvey et al. 2004; Magoulick 2004; Sunardi et al. 2007b).

Studies manipulating avian predation pressure on stream fishes or assemblages (e.g., Allouche and Gaudin 2001; Steinmetz et al. 2003, 2008) have also taken place since the publication of Matthews (1998). In addition to using different species, recent experiments tend to include more diverse predator and prey assemblages and have on occasion tested for emergent impacts of multiple predators (Figure 3). Other areas indicated by Matthews (1998) as needing attention have seen limited or no advancement. For example, a large-scale experiment manipulating whole stream assemblages has not yet been published. Studies testing for indirect effects of predators on competitive interactions among fish species also are lacking for lotic systems (but see Blanchet et al. 2008).

It is worth noting that the vast majority of predation experiments in lotic systems are from temperate regions (Figures 3 and 4), and the tropical studies conducted to date are almost exclusively from small streams in Trinidad with very low predator and prey fish diversity. High taxonomic and functional diversity of fishes in the majority of tropical river systems (e.g., see Lowe-McConnell 1987; Winemiller 1991), not to mention high diversity of piscivorous birds, reptiles, and aquatic and terrestrial mammals, means that there are literally thousands of predator-prey combinations in many tropical river systems. Risk enhancement from multiple predators may be more commonplace in tropical rivers, and indirect effects of predator-prey interactions may ripple through much larger suites of species. Disentangling this complexity will be no small undertaking but will undoubtedly provide unique insight into the relationships between species/functional diversity and the direct and indirect outcomes of predator-prey interactions in fluvial ecosystems.

At present, the majority of experimental research on predator effects in lotic fish as-

semblages provides case studies of single predator-prey pairs at an isolated place and point in time. To move beyond this "case studies" status, future research on predator-prey interactions in lotic ecosystems should advance the following five themes: (1) linking predation experiments with theoretical models of fish assemblage structure and function, (2) integrating functional traits into studies of predator-prey interactions, (3) manipulating whole assemblages and testing multispecies interactions, (4) understanding the role of predation in human-modified ecosystems, and (5) developing and applying analytical approaches that facilitate integration among the previous themes as well as with observational field studies.

#### *Predation Experiments and Theoretical Models of Fish Assemblage Structure and Function*

Connell (1975) argued that addressing community structure and dynamics without examining effects of predation is a serious conceptual error. Similarly, predation experiments should be clearly linked to the environmental template in which species interactions occur. For most lotic systems, the environmental template may be primarily characterized by environmental heterogeneity and aspects of hydrologic variability and predictability. Integrating experimental studies of biotic interactions with investigations of abiotic drivers of fish assemblages is a necessary step to advance our understanding of the relative importance of abiotic and biotic interactions in determining attributes of lotic fish assemblages and under what conditions predation may be expected to play a strong role in communities.

Several conceptual models of community organization are particularly suitable as a theoretical basis for predation experiments. Menge and Sutherland (1987) proposed a

general model of community organization that includes three primary ecological processes: physical disturbance, predation, and competition. The Menge-Sutherland model is a suitable general framework for predicting the relative importance of predator-prey interactions in and among streams because of the emphasis on environmental stress and recruitment across trophic levels. Several other models specifically developed for lotic systems are also clearly important as theoretical frameworks for predation experiments. Poff and Ward (1989) proposed a stream classification model based on hierarchical ranking of temporal components of stream discharge (i.e., flow predictability, flood predictability, and flood frequency). In their model, biotic interactions are predicted to be important in mesic groundwater streams and seasonally important when flood predictability is high. The Poff-Ward model is conceptually similar to one proposed by Zalewski and Naiman (1984). Other models provide more explicit spatial context, emphasizing the heterogeneity and connectivity of lotic systems. Within a given stream for example (e.g., one of the streams in Poff and Ward 1989), the model of Schlosser (1987a) predicts that longitudinal increases in habitat complexity and pool development correlate with increasing importance of biotic interactions. Increasing to the basin scale, the influence of stream network structure on instream habitats, particularly at confluences (Benda et al. 2004), may result in predator transition zones differing in the type or intensity of predation pressure (Creed 2006).

The patch dynamics concept (Pringle et al. 1988; Townsend 1989; and recently reviewed by Winemiller et al., in press), one of at least four distinct models of metacommunity dynamics (Leibold et al. 2004; Holyoak et al. 2005; see also Falke and Fausch 2010, this volume), is perhaps the most robust framework for predation experiments in lotic

systems because it explicitly addresses the spatially heterogeneous and temporally dynamic nature of lotic ecosystems. For example, non-lethal effects of predators on prey (e.g., shifts in habitat use) often require a heterogeneous environment, and movement of individuals among patches may be mediated by predation risk (e.g., Gilliam and Fraser 2001). Dynamic aspects of assemblages related to migration of both prey and predatory species, such as large-scale seasonal migrations in tropical river basins, may lead to seasonally enhanced predation pressure from migratory piscivores along migration corridors, or mixed-species shoals of "sit and wait" predators may create patches of risk enhancement for migratory prey fishes. Temporally dynamic environmental conditions (e.g., high and low flows) often affect patch size and connectivity, including those that may serve as refugia from predation, and mediate the effects of predation risk within a given patch (e.g., Magalhães et al. 2002). Furthermore, local assemblage resistance or resilience to disturbance may be affected by the presence, density or diversity of predators (e.g., Magoulick and Kobza 2003), and different types of disturbances (i.e., pulses, presses, and ramps) may elicit different responses from predators and their prey (Lake 2000).

In the few studies that included treatments consisting of some modification of environmental conditions (e.g., water volume/flow, structural complexity; Table 1), significant environmental effects on the strength of predator-prey interactions were observed. Future studies should continue to explicitly test for effects of environmental conditions in predation experiments, especially hydrologic characteristics that affect habitat volume and patch connectivity, as well as habitat complexity, resource availability, and ecosystem productivity. Experimental manipulations of predator-prey interactions over large spatial scales are need-

ed, especially those that exceed multiple patch boundaries and measure response variables at multiple scales (e.g., patch and reach scales). Studies testing effects of predators on fish assemblages should also extend temporal scales of investigation, especially to examine effects of predators on fish assemblage resistance and resilience to disturbances such as floods and droughts. The relationship between predation and flood predictability (e.g., Poff and Ward 1989) is also an important topic that can be addressed experimentally. Additional experiments in medium to large rivers are necessary, in spite of the associated difficulties of working with larger and more species rich systems.

#### *Functional Traits of Predators and Prey*

Functional traits such as body size directly influence the outcome of predator–prey interactions. Quantification of a broader suite of functional traits for both predators and prey would facilitate mechanistic understanding of outcomes of predator–prey interactions and may allow for results of experimental studies to be extended beyond the scope of the particular species involved to other assemblages with comparable traits (see Frimpong and Angermeier 2010, this volume). In addition to body size, other functional traits could affect predator–prey interactions and may be easily quantified or classified, such as burst swimming speed, predator foraging mode, prey response type (e.g., hiding, schooling, jumping from the water), and coloration patterns. Prey naiveté in response to a nonnative predator may also be important for predicting outcomes of predator–prey interactions involving nonnative species, and the degree of prey naiveté may be classified such as in Banks and Dickman (2007). In addition to response of prey to predation threat, the strategic response of predators to prey behavior may be quantified (Lima 2002).

In addition to functional traits associated with predator foraging mode and prey response, quantification of life history traits (e.g., as in Winemiller and Rose 1992) of both predators and prey would facilitate predictive modeling of spatial and temporal trends in predation pressure and effects of predation on population dynamics. For example, temporal patterns of prey switching by predators in response to prey reproductive pulses, spawning aggregations, or reproductive migrations can be linked with measures of other functional traits such as body size and gape size (e.g., Hoeinghaus et al. 2006). Likewise, predators may cease feeding during certain periods associated with reproductive activity or exhibit dramatic changes in abundance at a location as individuals undertake reproductive migrations. Lethal or nonlethal effects of predators that reduce prey population density or growth should differentially affect population dynamics of species with different life history strategies (e.g., Winemiller 2005), which may feed back into trophic interactions (e.g., Winemiller 2007). Predation pressure (magnitude and functional aspects) is expected to differ during different life history stages (including eggs) and the resulting effects on community dynamics needs experimental investigation.

#### *Assemblage-Level Experiments and Multispecies Interactions*

Only a handful of studies on effects of predation on lotic fishes conducted to date have used relatively complete assemblages (e.g., Harvey 1991; Layman and Winemiller 2004). Such assemblage-level experimental manipulations of predator–prey interactions are urgently needed because the outcome of predator–prey interactions within a subset of available prey or potential predators may change in the context of whole assemblages. Extending the experimental scale up to the assemblage level will also

allow for testing relationships between species diversity and functional diversity and effects on predator–prey interactions (i.e., risk reduction or enhancement). Assemblage level studies also may lead to identification of a trait or suite of traits that are important determinants of predator–prey interactions that transcend species richness (e.g., body size, Layman and Winemiller 2004), an important consideration for species rich tropical systems. Introductions of nonnative predators provide some insight in this regard (Ross 1991), but appropriate preintroduction data and replication may be limiting, and introductions are often coincident with habitat alterations (Light and Marchetti 2007).

Future studies should include the larger suite of nonfish piscivores that are common in natural systems, such as birds, reptiles and amphibians, and aquatic and terrestrial mammals, as studies conducted with these taxa found significant effects on prey fish (e.g., Steinmetz et al. 2003, 2008). Functional traits of this broader suite of piscivorous species should be quantified in similar terms as piscine predators. Assemblage-level studies should not only focus on the fish assemblage and the broader suite of predators, but also on spatially and temporally variable components of the ecosystem that may mediate predator–prey interactions in the fish assemblage. For example, the role of spatiotemporal variation in the relative abundance of alternative food items, including terrestrially derived subsidies or migratory species (e.g., Flecker et al. 2010, this volume), on predator–prey interactions in stream fish assemblages should also be addressed. Many piscivorous fish may also consume invertebrates and switch prey with changes in relative abundances (e.g., Winemiller and Kelso-Winemiller 1996; Jepsen et al. 1997; Deus and Petrere 2003), and prey species may take greater risks in response to changing resource availability (Gilliam and Fraser 1987; Skalski and Gilliam 2002).

Studies directly assessing effects of multiple predators on prey are a recent advancement in predation studies of lotic fishes, although they are more common in studies with other taxa (e.g., stream invertebrates and grassland invertebrates, Vance-Chalcraft et al. 2004; Vance-Chalcraft and Soluk 2005; Schmitz 2007). Future research should continue to develop this area, with attention paid to underlying differences in null model selection and experimental design. Two different null expectations, based on additive and multiplicative models, have been used in studies testing for emergent impacts of multiple predators (Soluk and Collins 1988; Sih et al. 1998; Figure 2e). The null expectation from the additive model is simply the sum of the proportion of prey affected by each predator in independent treatments ( $p_a + p_b$ , where  $p_a$  and  $p_b$  are the proportion of prey affected by predator species A and B, respectively). This model is problematic in that it allows prey to be killed twice, which generates a bias towards perceiving risk reduction and may result in null expectations that exceed 100% (Sih et al. 1998; Figure 2e). The multiplicative model corrects for this additive problem and predicts the expected proportion of prey that survive both predators to be equal to  $(1 - p_a)(1 - p_b) = 1 - p_a - p_b + p_a p_b$ , and the proportion killed is therefore  $p_a + p_b - p_a p_b$  (Soluk and Collins 1988; Figure 2e). Experimental designs with multiple predators may increase predator density as a result of the additional predator or maintain predator density constant among independent and combined treatments (i.e., additive or substitutive designs; Griffen 2006; Figure 2f). Future studies should test both the additive and substitutive experimental designs simultaneously as they test different, but complementary, mechanisms and have different null expectations and interpretations (Figure 2f; see Sih et al. 1998; Vance-Chalcraft et al. 2004; Griffen 2006; Schmitz 2007).

In addition to continuing research on multiple predator effects on a single prey species, future studies should address indirect effects of trophic interactions within stream fish assemblages, such as exploitative competition, apparent competition, and indirect mutualisms (Figure 1d–h). For instance, reduced abundance or behavioral change in a potential competitor may affect growth and reproduction of a focal species, or reduced abundance of one prey species may cause increased predation risk for other species. Understanding the outcomes of indirect interactions will be critical as more complex fish assemblages are used in predation experiments. Furthermore, quantification of the direct and indirect effects of a species should help predict the community and ecosystem responses to its extirpation or change in abundance (e.g., key consumer in a trophic cascade; Power et al. 2008).

#### *Anthropogenic Impacts and Predator–Prey Interactions*

Experimental investigations of predator–prey interactions expressly considering anthropogenic changes to fluvial ecosystems are urgently needed. Most fluvial systems have been impaired to some degree, and relationships between predators and prey are likely to have been significantly modified by the altered environment. Because the role of predation is predicted to increase with hydrologic stability (Poff and Ward 1989), the pervasive anthropogenic impacts that stabilize hydrologic regimes (e.g., river impoundment, runoff acquisition, and water withdrawal) should increase the role of predation in structuring lotic fish assemblages. For instance, piscivore fish species richness and biomass increased in the years following construction of large dams in neotropical river basins (Mérona et al. 2001; Agostinho et al. 2007a). In addition to the flooded area, a sharp increase in predation pressure may appear in adjacent

environments, such as downstream from dams and near fish passages (e.g., ladders). These locations seem to attract large, functionally diverse aggregations of piscivores (e.g., Blackwell and Juanes 1998; Agostinho et al. 2007b; authors' personal observation) and may be hotspots of emergent impacts. Furthermore, hydrologic alterations (e.g., river impoundment) facilitate species invasions in fluvial ecosystems (Gido and Brown 1999; Havel et al. 2005; Johnson et al. 2008). Nonnative piscivores adapted to modified (stable) hydrologic conditions have the potential to exert swift and strong top-down effects on native fish assemblages (e.g., Pelicice and Agostinho 2009).

In addition to the indirect effects of humans on predator–prey interactions via habitat alteration, humans act directly as predators of lotic fish assemblages through fishing (Allan et al. 2005). Inland fisheries are typically very selective (e.g., Petrere et al. 2004, Agostinho et al. 2007a), targeting large-sized individuals, especially piscivore species with migratory behavior (e.g., catfishes and large characins in tropical rivers; Hoeinghaus et al. 2009). Similar to experimental studies with animal predators, natural and manipulative experiments of selective fishing (mostly in marine ecosystems) have found significant shifts in assemblage composition, size structure, and population life history traits (e.g., Conover and Munch 2002; Birkeland and Dayton 2005). Similar experiments may be designed to test effects of selective harvest on fluvial populations. In addition to direct effects on fishery species, fisheries may cause an indirect decrease in natural predation pressure on other members of the fish assemblage as a result of selective removal of top predators.

#### *Analytical Techniques and Applications*

Expanding the scope of future studies to more diverse assemblages and incorporating environmental drivers creates analytical and logis-

tic concerns regarding the ability to identify causal relationships and disentangle effects attributable to different factors. One promising approach that has not been embraced in previous studies (but see Blanchet et al. 2008) is integrating field measures of environmental variables (e.g., availability of cover/space, water velocity) and one or more experimental manipulations of the assemblage (e.g., predator exclusion) with path analyses and model selection criteria (Wootton 1994a). This analytical framework may allow for predicting and testing both direct and indirect interactions within an assemblage (including species not individually manipulated) using a limited number of experiments (Wootton 1994a). Bioenergetics models (e.g., Muhlfeld et al. 2008; Dalton et al. 2009) may also be incorporated into a broader experimental research program investigating predator–prey interactions to help scale up experimental findings.

Incorporating quantitative measures of species functional traits will also enable application of analytical techniques previously outside the realm of predation experiments in lotic systems. For example, new response variables in studies quantifying a suite of functional traits of predators and prey could include aspects of functional diversity (i.e., functional richness, evenness, or divergence) of the assemblage in response to predation based on a single trait (Mason et al. 2005) or a combination of multiple traits (e.g., Cornwell et al. 2006; Villéger et al. 2008). Generalist predators may be predicted to have no discernable effect on functional diversity of the assemblage, whereas more specialized predators, such as in relation to body size or prey type (e.g., benthic, pelagic), may be expected to reduce functional diversity of the assemblage in different ways.

The relative importance of lethal versus nonlethal effects of predators on prey (e.g., relative contributions of consumption and

emigration in reducing prey density) is an important distinction that should be given more attention in future research. Nonlethal effects of predators may play an integral role in local communities and metacommunity dynamics that is easily overlooked or difficult to identify unless acting in a direction opposite of lethal effects (Orrock et al. 2008; Peckarsky et al. 2008). A fuller appreciation of nonlethal effects of predation will facilitate linking experimental research on predator–prey interactions with field studies or analyses attempting to estimate the relative importance of environmental variation and biotic interactions (e.g., Grossman et al. 1998; Hoenighaus et al. 2007).

As more predation studies in lotic fish assemblages are conducted, specific null hypotheses of predation effects on different response variables can be tested across studies via meta-analysis (Osenberg et al. 1999). Similar to recent meta-analyses of biodiversity–ecosystem function experiments (Balvanera et al. 2006), meta-analysis of effect sizes in predation experiments would provide statistical rigor to some of the generalities identified herein, as well as test new hypotheses emerging from future work. Meta-analyses of predation effects on lotic fish assemblages should test for differences in effect sizes (including distinction of lethal versus nonlethal effects) among predator taxa and functional groups, among ecosystem types (e.g., temperate versus tropical), and in relation to predator and prey species richness or functional diversity.

## Conclusions

Three decades of experimental investigation in dynamic lotic environments indicate that predation can exert strong, and often predictable, effects on prey fishes and assemblages. Recent studies have employed a wider variety of experimental designs and tested more response

variables with larger numbers of species. Future research integrating experimental studies of biotic interactions with investigations of abiotic drivers of fish assemblages is necessary to advance our understanding of the relative importance of abiotic and biotic interactions in determining attributes of lotic fish assemblages and under what conditions predation may be expected to play a strong role in communities and ecosystems. Integrating ecological theory, environmental variability, functional traits of predators and prey, and more complex assemblages and analyses will help the next generation of predation experiments make the leap from “case study” to “ecological concept.”

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