pp 333-351 in W.C. Kerfoot and A. Sih (eds.) Predation
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22. Predator Avoidance by Grazing Fishes in Temperate and Tropical Streams: Importance of Stream Depth and Prey Size

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Grazing fishes can strongly affect benthic algal distributions in streams. Distributions of grazing fishes along depth gradients and among pools in streams appear constrained by depth- and size-specific predators. Large (>3 cm long) grazing fishes avoid shallow (<20 cm) water, where wading and diving predators feed most commonly and effectively. As a result, bands of algae are maintained along shallow stream margins in a secondary rain forest stream in Panama and in a prairie-margin stream in south-central Oklahoma, despite intense grazing and scant algal standing crops in deeper areas. Small (<3 cm long) grazing fishes, postulated to be less susceptible to wading and diving predators and more susceptible to swimming predators, were more abundant than large grazers in shallow water in Panamanian and Oklahoman streams. Shallow areas appear to be refuges from competitors and swimming predators for small grazers, which were nonetheless limited at densities below those necessary to deplete shallow algae. "Bigger-deeper" distributions of grazing catfishes in a Panamanian stream remained unchanged from the rainy to the dry season during 2 years, despite a two- to three-fold contraction of "critical habitat" (streambed under >20 cm) and evidence from somatic growth rates of increasing food limitation.

On a larger scale, grazing fishes affect variation in algal standing crops among stream pools, as well as along depth gradients. In the Rio Frijoles of central Panama, algal standing crops were uniformly low in pools, despite large differences in primary productivities related to forest canopy cover. Large armored catfish in this stream appeared able to outgrow most swimming predators and could move among pools sufficiently to track and damp out incipient variation in algal standing crop. In contrast, pool-to-pool variation in algal standing crop was amplified by grazing minnows (*Campostoma anomalum*), which were excluded from some pools by piscivorous bass.

Grazing fishes in both Panama and Oklahoma avoid foraging in dangerous areas (shallow water, bass pools), even when their algal food is abundant there and scant elsewhere. Depth and size-specific predators, by restricting access to food for grazing stream fishes, can influence their demographic rates, carrying capacities of streams for their populations, and their effects on stream flora. Where grazing fishes are important, experimental studies of the effect of stream depth, an easily measured and manipulated variable, on foraging by grazing fishes and their predators should provide much insight into the complex ecological consequences of a single environmental variable.

Grazing fishes are abundant in many temperate and tropical streams, and are potentially voracious consumers of algae. Algae, in turn, can grow rapidly. High rates of algal growth and fish consumption often couple to produce patterns in streams that reveal the spatial distribution of herbivory. What behaviors and constraints underlie the distributions of grazing fishes in streams? Most streams meander and are therefore made up of sequences of pools separated by shallower riffles. Pools are habitats for larger species and size classes of stream fish. What factors control fish densities in particular pools relative to others in the stream? Can grazing fishes track pool-to-pool variation in resources such as food? To what extent are fish distributions constrained by factors like predators? One can ask similar questions about distributions of fishes within stream pools: along depth gradients or on different substrates. To answer these questions, one must learn about the risks and opportunities for fish in stream environments and also about fish capabilities. How mobile are grazing fishes and their predators; in particular, what are thresholds that determine whether they will cross barriers such as riffles? How good are their perceptions and memories of resource availability or predation risk? What compromises will they make when resource acquisition and risk avoidance require different behaviors? Do tradeoffs vary with hunger, age, body size, season, or among species?

Predators have been shown or postulated to restrict the foraging areas of their prey in marine and freshwater habitats (Stein and Magnuson 1976; Sih 1982; Seghers 1970; Randall 1965; Stein 1979; Cooper 1984; Garrity and Levings 1981; Mittelbach 1984; Werner et al. 1983; Power 1984a). By making portions of habitat too dangerous to use, predators may limit food available to prey and alter the effects of these prey on their communities. When fish that graze benthic algae avoid certain areas, the algae released from grazing often attain conspicuous standing crops (Randall 1965; Ogden and Lobel 1978; Power and Matthews 1983; Power et al., 1985). Clear patterns, such as grazed "halos" around rubble cover in coral reefs (Randall 1965) or bands of algae along stream margins (Power 1984a) may indicate the spatial distribution of predator-induced resource avoidance by grazing fishes (Ogden and Zieman 1977; Earle 1972; Hay 1984 and references therein). Significant indirect effects on other biota may result, because ungrazed algae may physically modify the habitat and provide food or cover for a wide range of organisms (Estes and Palmisano 1974; Duggins 1980; Paine 1980; Hynes 1970).

Here I will describe patterns of distribution of algae-grazing fishes, their algal food, and their predators in streams in Panama and Oklahoma. Armored catfish of the family Loricariidae graze algae in the Panamanian stream, whereas Oklahoma streams are grazed by schools of the minnow *Campostoma anomalum*. I will focus this review on distribution patterns of fish and algae that occur on two spatial scales: within pools along depth gradients, and among pools. Grazing minnows and armored catfish are constrained by predators with depth-specific foraging rates on some scales but not others. The presence or absence of such predators can account in large part for the distribution and effects of these grazing fishes in stream communities.

DEPTH DISTRIBUTIONS OF GRAZING FISHES WITHIN STREAM POOLS

A very widespread pattern in fish assemblages is that small species and size classes occupy shallow habitats, and larger individuals occur at greater depths. This "bigger–deeper" distribution has been documented for fish in marine (Fishelson et al. 1971; Clarke 1977; Hobson 1968, 1974), estuarine (Hellier 1962), and freshwater (Hall 1972; Keast 1978; Werner et al. 1977; Bowen 1979; Jackson 1961) habitats (see Helfman 1978 for a review). The bigger–deeper distribution is well illustrated by four species of armored catfish (family Loricariidae) that graze algae in the Rio Frijoles of central Panama (9° 9'N, 79° 44'W). Large, noncryptic loricariids (*Ancistrus spinosus*, *Hypostomus plecostomus*, and *Chaetostoma fishcheri* > 5 cm SL) are rarely found in water < 20 cm deep and are most common at depths > 40 cm. Juveniles of these species and 2- to 7-cm long members of a thin cryptic species, *Rineloricaria uracantha*, occur frequently in water < 20 cm deep and are most common in depths < 40 cm (fig. 22.1; also see Power 1984a). Loricariid depth distributions were seasonally invariant despite a two- to three-fold contraction of stream habitat (area > 20 cm deep) from the rainy to the dry season (Power 1984a, and discussed below).

Similar patterns with depth occur among size classes of the grazing minnow *Campostoma anomalum* in prairie-margin and Ozark upland streams of Oklahoma. A school of adult *Campostoma* (> 4 cm SL) was observed on 20 occasions over a 6-day period in a stream pool where they were free of swimming predators. These *Campostoma* occurred in water > 20 cm deep on 20/20 scan samples, and in > 30 cm of water on 18/20 scans. In contrast, young-of-the-year *Campostoma* (2–3 cm SL) in the same pool were in water < 20 cm deep on 4/14 scans and were in < 30 cm of water on 6/14 scans (Power et al. 1985). Similar bigger–deeper patterns were seen in the distribution of size classes of *Campostoma* in a pool of Tyner Creek, an Ozark stream in northeast Oklahoma (Matthews et al., in press).

The bigger–deeper distributions of fish in

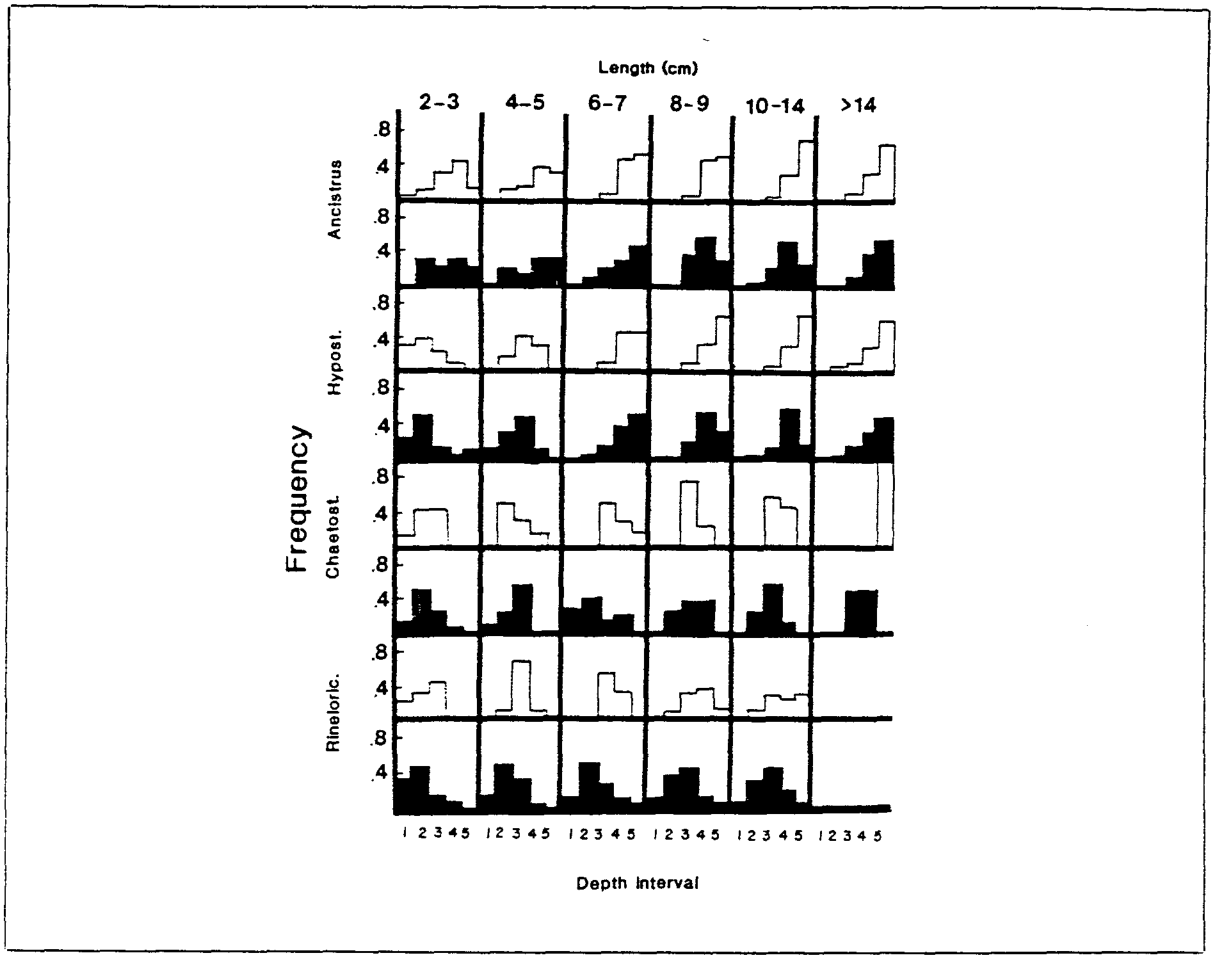

Figure 22.1. *Proportions of various species and size classes of loricariids that occurred within five depth intervals by day* (open bars) *and by night* (solid bars). *Loricariids were counted during two rainy-season, two dry-season, and two transitional-season census series of 150–168 L/m² quadrats; proportions averaged from a total of 1,516 day quadrat counts and 1,412 night quadrat counts are plotted here. Depth intervals: 1 = <10 cm; 2 = 10–20 cm, 3 = 21–40 cm; 4 = 41–80 cm; 5 = >80 cm.*

streams and other aquatic habitats is consistent with the hypothesis that water depth and body size interact to influence vulnerability of fish to predators. Observations, and limited experimental evidence, suggest that fish in shallow water (<20–30 cm) are more susceptible to wading or diving predators, whereas fish in deeper water are more susceptible to swimming predators. Moreover, wading and diving predators may take larger prey than "gape-limited" (Zaret 1980) swimming predators in streams. Where these conditions hold, large stream fish should avoid shallow areas, and small fish should avoid deep areas to reduce exposure to their most important predators.

There is much evidence that large, piscivorous fish exclude small fish from deep, open water (Jackson 1961; Goodyear and Ferguson 1969; Seghers 1970, 1974a; Goodyear 1973; Werner et al. 1977, 1983; Keast 1977; Mittelbach 1984; Power 1984a). Small fish emerge from littoral vegetation in tropical and temperate lakes when they have attained sizes at which they are less vulnerable to predatory fishes in deeper open habitats (Jackson 1961, Werner et al. 1983). Riffles in the Rio Frijoles of Central Panama are nursery areas for small (<4 cm) armored catfish (family Loricariidae) which, when they are placed in deeper pools, are readily eaten by larger fish (Power 1984a). Shallow edges of pools in Brier Creek, Oklahoma, serve as refuges for larvae and young of the year of both minnows and centrarchids subject to predator by larger centrarchids in deeper areas (B. Harvey, unpublished data, personal observations).

Although there is ample evidence that swimming predators can exclude small fish from deeper habitats, evidence that wading and diving predators exclude larger fish from shallow habitat is, to date, largely circumstantial (e.g., Power 1984a). The potential threat to fish in shallow water from birds is apparent from severe depredations that occur when fish are concentrated artificially in shallow hatching pools (Kushlan 1978; Lagler 1939; Mott 1978; Naggiar 1974), or naturally in shrinking tropical stream pools during the dry season (Lowe-McConnell 1964, 1975; Williams 1971; Bonnetto 1975). Bird predation caused a 77% decrease in numbers of fish in a small Florida pond when water level dropped during the dry season (Kushlan 1976). Some experimental evidence also suggests a depth gradient in risk of predation for large fish. I tethered 20 large (7–16 cm SL) armored catfish (*Ancistrus spinosus*) in the Rio Frijoles, in water 11 to 25 cm deep, where herons and kingfishers had been seen fishing. After 24 hours, 0/6 catfish that had been tethered in water < 18 cm deep remained, whereas I recovered 10/14 catfish tethered in water ≥ 18 cm deep ($p = 0.005$; Fisher's Exact Test). In a subsequent experiment, size-matched groups of armored catfish were enclosed in open-topped pens that were similar in surface area and substrate but set at different depths in the stream. After 12 days, during which little blue herons (*Egretta caerulea*) were sighted foraging within a meter of one series of pens, loricariids were largely eliminated from those in 10 and 20 cm of water, but most remained in pens in 30 and 50 cm (Power, Dudley, and Cooper, unpublished data).

If diurnally foraging birds exclude fish from shallow water, fish depth distributions may change at night. Starrett (1950) observed minnows moving by night to forage in shallower parts of an Iowa stream. There was a slight (but insignificant) tendency for armored catfish in Panama to move into shallower water by night (fig. 22.1). Nocturnal movements of loricariids might have been inhibited by night-fishing tiger herons (*Tigrisoma rufescens*) and mammals around the Rio Frijoles (Power 1984a).

INFLUENCE OF SWIMMING PREDATORS ON DISTRIBUTIONS OF GRAZING FISHES AMONG STREAM POOLS

Bigger–deeper distributions of fish occur among pools in streams, as well as along depth gradients within them. Larger predatory fishes often occupy deeper stream pools, leaving shallower pools as potential refuges for smaller grazing species. Largemouth and spotted bass (*Micropterus salmoides* and *M. punctulatus* > 7 cm SL) are the major swimming predators of grazing minnows (*Campostoma anomalum*) in Brier Creek, Oklahoma. In a 1-km reach of Brier Creek, containing 14 pools, distributions of bass and *Campostoma* and maximum depths of stream pools sometimes changed, particularly after large floods (Power et al. 1985). During eight snorkelling censuses of the 14 pools conducted over a 2½-year period, large bass occurred in pools ≥ 50 cm deep on 72 pool-dates and were in shallower pools on only 3 occasions. The total occurrences of deep and shallow pools on the eight dates were 86 and 25, respectively, suggesting selectivity by bass for deeper pools (χ^2, 10.6; $p < 0.01$) *Campostoma* occurred in deep pools on 29 occasions and in shallow pools on 27 occasions. These minnow did not select shallow pools per se (χ^2, 0.42; $p > 0.50$), but their distributions among pools in Brier Creek were significantly complementary with those of large bass, which did select deeper pools, on seven of eight censuses (Power and Matthews 1983; Power et al. 1985, unpublished data). In one long pool where bass and *Campostoma* often co-occurred, they were spatially segregated with bass near the area of maximum depth, and *Campostoma* (and other minnows) in the long, shallow tails (Power and Matthews 1983; W. J. Matthews, B. Harvey, and M. E. Power, unpublished data). In pools that lacked bass, however, *Campostoma* spent most of their time in deepest areas.

These patterns suggest that large bass displace *Campostoma* from deeper pools and pool areas. During spring and autumn experiments, largemouth bass (18–28 cm SL) were introduced into a pool that formerly had contained *Campostoma* and no bass. Prior to bass addition, adult *Campostoma* had spent most of their time foraging over substrates in the

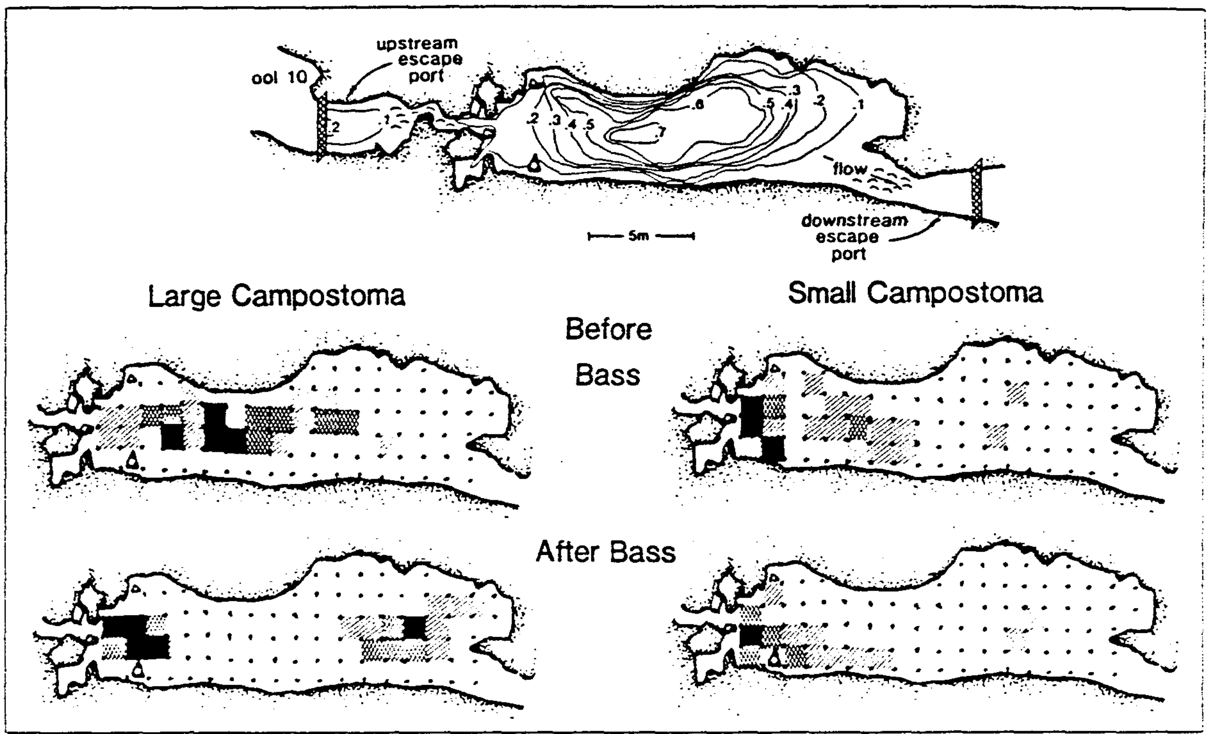

Figure 22.2. *Space use by large (4–8 cm SL) and young of the year (2–3 cm SL)* Campostoma *in a pool before and after the addition of two largemouth bass* (Micropterus salmoides, *18 and 23 cm SL). The pool floor was marked with concrete nails into a grid of squares, 1 m on each side (indicated by dots). The numbers of sightings of* Campostoma *within a particular square meter on scan samples carried out on 6 days before and 7 days after bass addition is coded as follows:* solid, *5 or more sightings;* cross-hatched, *3–4 sightings;* single-hatched, *1–2 sightings.*

deepest parts of the pool (40–60 cm deep; fig. 22.2). After bass addition, these minnows were displaced within hours to shoals < 20 cm deep, while bass occupied the deepest area in about 60 cm of water (fig. 22.2, table 22.1; Power et al. 1985). During the spring experiment, *Campostoma* young of the year (2–3 cm TL) were present. Bass addition did not significantly change their depth distributions (fig. 22.2). Before bass addition, these small *Campostoma* had already occupied shallower habitats than did adults in the pool. At that small size, young of the year were subject to attack by sunfish (*Lepomis* spp.) in deeper areas (B. Harvey, unpublished data).

Predator avoidance by *Campostoma* and predation by bass both contributed to their complementary distributions among stream pools. Before experimental additions of bass to a pool in Brier Creek containing *Campostoma*, we blocked off adjacent portions of upstream and downstream pools, so that emigrating fish could be recovered. During fall experiments, 7 of 70 *Campostoma* were recovered from a blocked "escape port," which they had reached by crossing a narrow channel 2 m long and < 10 cm deep. This number may underrepresent the actual emigration, as the block net was displaced during a spate. Nets remained in place throughout the course of a spring experiment. Forty of 74 adult (4–8 cm SL) *Campostoma* originally in the pool were recovered in an "escape port" 6 hours after bass addition (Power et al. 1985). After 1 week, 19 adult *Campostoma* and 13 juveniles (2–3 cm SL) were unaccounted for and were presumed to have been eaten by the bass.

Campostoma are soft, thin fish that remained vulnerable to bass in Brier Creek throughout their lives. In contrast, large loricariids are well defended by spines and dermal armor, and they seemed able to outgrow most swimming predators in the Rio Frijoles. Four *Ancistrus*, 16 to 18 cm SL, developed eye lesions and became increasingly easy for me to capture. Yet I continued to sight these individuals for periods up

Table 22.1. *Remains of loricariids found along Rio Frijoles, presumed killed or mangled by predators*

Species, std. length	Wounds	Probable predator
Ancistrus, 15 cm	Triangular peck wounds, belly and head gone	Bird
Ancistrus, 10 cm	One triangular wound, 1.3 cm wide, through dorsal carapace	Bird
Ancistrus, 9 cm	Two round punctures, 1 mm diameter, spaced 2 cm apart	Mammal
Ancistrus, 14 cm[a]	Body gone except for head and left pectoral spine	Bird or mammal
Ancistrus, 13 cm[a]	Body gone except for chewed tail	Mammal
Ancistrus, 12 cm	Head bitten off	Bird or mammal
Rineloricaria, 12 cm	Two punctures, 1 mm wide, spaced 1 cm apart, above right pectoral fin	Fish or snake
Chaetostoma, 4 cm	Tail gnawed to stump, snout chewed	Mammal

[a] Length estimated from remaining body parts.

Maximum standard lengths (cm) of loricariids found in Rio Frijoles: *Ancistrus*, 20 cm; *Hypostomus*, 30 cm; *Chaetostoma*, 17 cm; *Rineloricaria*, 12 cm.

to 10 months after I first noticed their disease, a circumstance highly unlikely to occur had they been subject to predation. Large loricariids may have been nearly free of predators in deeper areas of the Rio Frijoles, but they could not outgrow vulnerability to predators that foraged in shallow areas. If captured, even the largest Rio Frijoles loricariids could be torn apart by birds or mammals, as evidenced by occasional fresh body fragments of the largest, most heavily armored size classes found along stream banks (table 22.2, fig. 22.3). Their freedom from swimming predators, however, enabled loricariids to move among pools in their stream and choose habitats on the basis of food availability, a prerogative with important consequences for algae in their stream.

EFFECTS OF GRAZING FISHES ON DISTRIBUTIONS OF STREAM ALGAE

Presence or absence of swimming predators that constrain their pool-to-pool distributions determines how grazing fishes will affect large-scale distributions of stream algae. Armored catfish, after they outgrow swimming predators, can move among pools and track variation in algal availability. Where forest canopy over pools is open and algal growth rates are high, grazing catfish are more dense than they are in dark, relatively unproductive pools. In fact, catfish are roughly six to seven times denser in sunny pools where algae grow about seven times faster than in dark pools (Power 1983, 1984b). Movement among pools is required to maintain this pattern, as algal productivity can change abruptly—for example, when a tree falls open-canopy over a pool or when pools are created or filled during floods. Because loricariids can find and exploit new feeding opportunities within weeks after they arise, these grazing fishes damp out incipient pool-to-pool variation in algal standing crop. As a result, standing crops of algae are uniformly scant among pools in the Rio Frijoles of Panama, despite large differences in primary productivity of algae in different pools (Power 1984b).

In marked contrast, striking variation in algal standing crop occurs among pools in Brier Creek, Oklahoma. Some pools are nearly barren, except for fringes of algae around their shallow margins. These barren pools contain schools of *Campostoma* and lack bass. Other, often adjacent pools that lack *Campostoma* and contain bass are at times nearly filled with filamentous green algae (*Rhizoclonium* sp. and *Spirogyra* sp.). Experimental transfers have shown that *Campostoma*, when introduced into pools from which bass have been removed, can denude large standing crops of algae in bass pools

Table 22.2 *Numbers, depth and activity of bass and minnows* (Campostoma anomalum) *before and after introduction of bass to a* Campostoma *pool*

		Campostoma				Bass	
	Numbers sighted	% in various depths activity					
		< 20 cm	20–30 cm	> 30 cm	Activity	Depth	Activity
9 Sept (a.m.)	70	0	0	100	Grazing		
15:00: Introduction of two bass, 18 and 23 cm SL							
15:30	70	0	0	100	Schooling	60	hiding
17:30	70	0	100	0	Grazing	60	hiding
10 Sept							
10:00	70	15	85	0	Milling	60	hovering
12:45	70	100	0	0	Milling	30–40	patrolling
13:19		100	0	0	Milling	60	hovering
16:35		100	0	0	Milling	60	hovering
13 Sept							
11:00	11	100	0	0	Milling	30–40	patrolling
12:00	11	100	0	0	Milling	30–40	patrolling
17 Sept: Bass escape during spate; replaced by two of same size							
18 Sept							
before bass added		0	0	100			
immediately after		100	0	0			
24 Sept							
15:20	12	100	0	0	Hovering	30–40	patrolling
7 *Campostoma* recovered from upstream escape port							
26 Sept	0					60	hovering
1 Oct	0					60	hovering
3 Oct	0					60	hovering
13 Oct Snorkeling census reveals 11 inactive *Campostoma* under cobbles, 10–20 cm deep							

within weeks. Similarly, when *Campostoma* grazing is inhibited by the introduction of bass into their pools, algal standing crops recover within weeks to levels typical of bass pools (Power et al. 1985). Consequences of the extreme pool-to-pool heterogeneity in algal standing crops that results from this predator–prey interaction for nutrient uptake and regeneration in Brier Creek are presently under investigation (A. J. Stewart, personal communication).

Whereas armored catfish in the Rio Frijoles and grazing minnows in Brier Creek produce opposite effects on pool-to-pool distributions of algae, they produce similar patterns within pools. In *Campostoma* pools of Brier Creek and throughout the Rio Frijoles, algal standing crops are often relatively high in water < 20 cm and decrease sharply at greater depths (fig. 22.4). This depth threshold corresponds to the depths at which wading and diving birds forage most frequently and effectively (discussed below). Avoidance of these predators by both grazing minnows and catfishes is one explanation for higher standing crops of algae in shallow water. Light and nutrient availability is usually higher in shallow water, and differences in algal productivity also could produce depth gradients in standing crop. This explanation cannot, however, account for algal distributions along depth gradients in bass pools of Brier Creek. Algal standing crops in bass and *Campostoma* pools are similar in shallow water, but increase then asymptote with depth in bass pools, in contrast to standing crops in *Campostoma* pools that drop off abruptly in depths > 10 cm (Power and Matthews 1983: fig. 3). In bass pools that lack *Campostoma*, standing crops of algae are higher in water 11 to 60 cm deep than in wa-

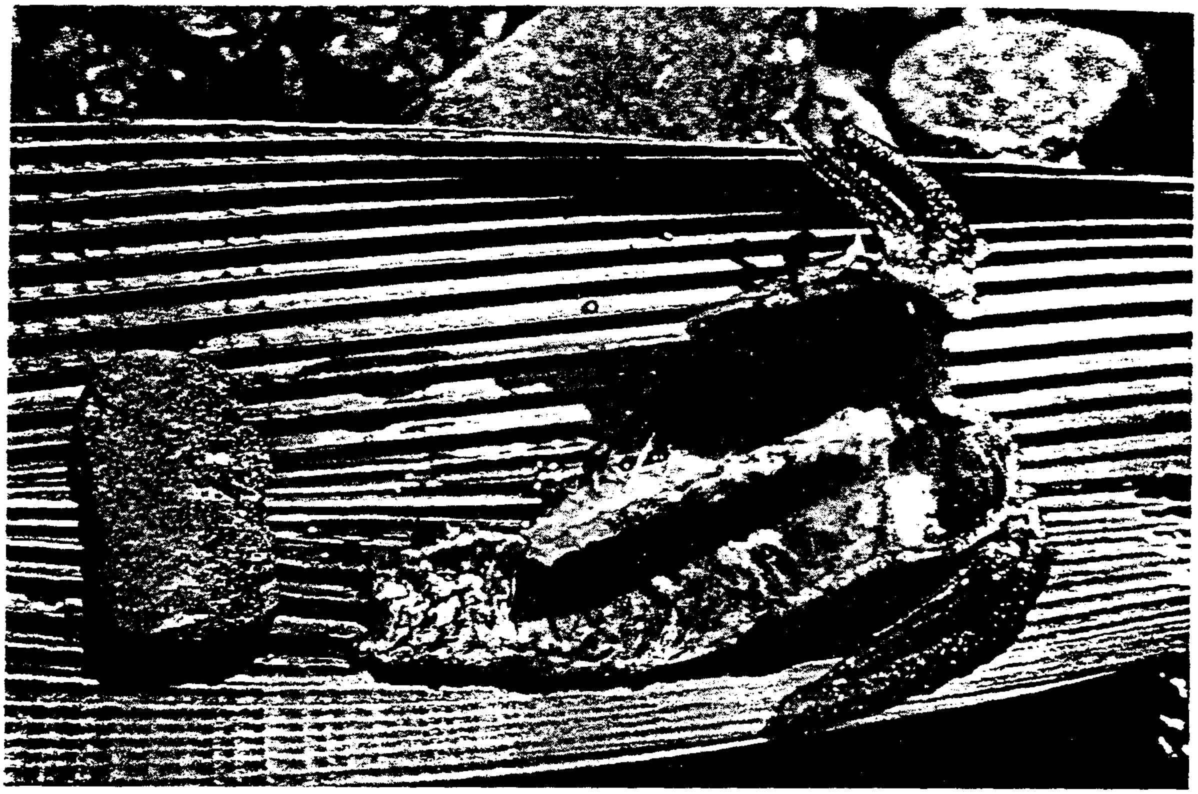

Figure 22.3. *Remains of large loricariids found along banks of the Rio Frijoles. The stone on the leaf with the fresh, empty loricariid carapace is 6 cm wide.*

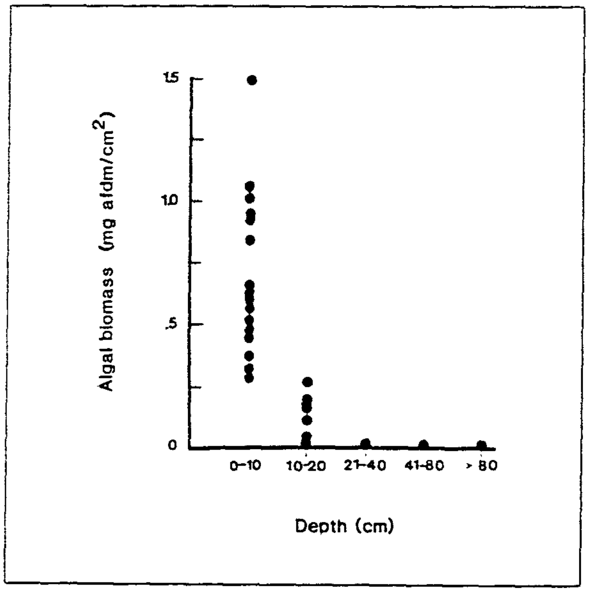

Figure 22.4. *Periphyton standing crops (ash-free dry mass) sampled from cobbles collected haphazardly from various depth intervals during the late dry season (March) in the Rio Frijoles, Panama. Sample sizes are* N *= 17 (< 10 cm);* N *= 9 (10–20 cm);* N *= 10 (21–40 cm);* N *= 11 (41–80 cm);* N *= 10 (> 80 cm).*

ter 0 to 10 cm deep ($p < 0.01$, Mann-Whitney U-test). The reverse is true in pools with *Campostoma* ($p < 0.03$, Mann-Whitney U-test. Brier Creek is frequented by raccoons (*Procyon lotor*), green herons (*Buturoides striatus*), belted kingfishers (*Ceryle alcyon*), and great blue herons (*Ardea herodias*; we commonly see tracks of these herons along shallow stream margins). Avoidance of depth-limited predators by *Campostoma* in Brier Creek and by loricariids in the Rio Frijoles may contribute to the maintenance of bands of algae along margins of pools in both streams.

COSTS OF PREDATOR AVOIDANCE FOR GRAZING STREAM FISHES

Predator-induced avoidance of dangerous feeding areas can impose energetic costs on food-limited prey (Sih 1982; Werner et al. 1983; Cooper 1984). For prey whose vulnerability changes with size, distributions of food and predation risk over the habitat can determine in large part the three fundamental demographic rates: size-dependent growth, size-dependent fecundity, and size-dependent mortality (Werner and Gilliam 1984). In size-structured populations, some size-classes may be more food-limited than others that have outgrown predators. Bluegills (*Lepomis macrochirus*) in experimental ponds in Michigan became less food-limited as they outgrew bass and moved from littoral vegetation into limnetic areas where they foraged more profitably (Werner et al. 1983; Werner and Gilliam 1984; Mittelbach 1984). In contrast, armored catfish became more food-limited as they grew and moved out of shallows of the Rio Frijoles, where algal standing crops were higher. To illustrate the size-dependency of their vulnerability and access to food, I will describe the life cycle of the most common loricariid in stream pools: *Ancistrus spinosus*.

Ancistrus begin their lives as eggs in their father's nest, typically a hollow log in a deep pool. He serves as an armored cork, blocking the nest entrance against potential egg and fry predators such as freshwater crabs (*Potamocarcinus richmondi*) and characin fishes. Hatchlings stay with their father until they are about 18 mm SL. Although a "fledging episode" of *Ancistrus* has not to my knowledge been observed in nature, it is likely that the young face a gauntlet of swimming predators when they leave the nest. Stream pools in the Rio Frijoles are densely populated by characin fishes, active by day and night, that devour *Ancistrus* 2 to 3 cm long when these are introduced into pools (Power 1984a). Young *Ancistrus* that survive enter shallow stream riffles, where the highest algal standing crops in the stream channel occur. The three noncryptic loricariids graze and grow in these shallow nursery areas until they are 3 to 4 cm long. (The cryptic *Rineloricaria* can be found in riffles until it is about 8 cm SL.) At this size, they begin to outgrow refuges available in the interstices of riffle cobbles and probably become more conspicuous to herons and kingfishers that commonly fish water <20 cm deep in the Rio Frijoles (Power 1984a). They also become less vulnerable to most swimming predators in the pools. At 4 to 5 cm SL, the catfish move into deeper habitats. After attaining lengths >5 cm, *Ancistrus* avoid water <20 cm deep by day and night, even during the dry season when algal food is abundant there and in short supply in deeper areas (Power 1984a).

Large loricariids (the three noncryptic species >5 cm SL collectively made up 83% of the loricariid biomass in the Rio Frijoles) were food-limited for much of the year. In contrast to shallow algae, algae in deeper water had standing crops so scant that measurable amounts could not be scraped from any substrate in >20 cm of water within a 2.8-km channel at any season over a 2-year period (Power 1981). A total of 1,308 loricariids were individually marked and periodically recaptured to measure growth. Prereproductive *Ancistrus* (4–9 cm SL) showed their highest growth rates when early rainy season floods gave fish first access to algae in areas previously too shallow to graze. Growth declined but remained positive during the latter part of the rainy season (July–November) and stopped during the dry season (December–early April) (Power 1984a). [When deprived of food, loricariids lose fat but not live weight (Power 1984c). They may replace catabolized tissue with water, as do other fish.]

Loricariid catfish <4 cm SL were too delicate to mark with the technique I used, so growth data are not available for these small size classes. Higher standing crops of algae in their shallow habitats, however, suggests that small loricariids were not as food-limited as larger individuals in the more barren pools.

Because of their restricted depth distributions, it was possible to estimate seasonal food availability for particular species and size classes of loricariids. This food availability depended on the area and primary productivity of streambed within the depth interval grazed by given catfish. From a detailed bathymetric map (10-cm contour intervals) of the 2.8-km study reach and a hydrograph record for a 24-month period, I computed the area of streambed under various depths for periods of high (July–November), low (March–early April), and intermediate (January, June) flow. Taking into account the area of streambed under forest canopy that was <10% 10 to 25%, 26 to 50%, and >50% open; growth rates of stream algae under each canopy; light attenuation in the water column; and the proportions of grazeable substrate (excluding mud and sand), I estimated the daily renewal rate of algal organic matter available to loricariids within each depth interval (Power 1981: tables 2-4, 2-5, and 4-5). These estimates were compared with collective metabolic requirements of species and size classes of loricariids that grazed within each depth interval. I estimated numbers of loricariids with data from six series of 2 day and 2 night censuses over the 2.8-km reach. Census series were carried out during two dry, two rainy, and two transitional season periods over a 28-month period. Length–weight regressions, based on 159, 91, 50, and 41 measurements for *Ancistrus*, *Hypostomus*, *Chaetostoma*, and *Rineloricaria*, respectively, were used to estimate weights for loricariids in each length class. (Length : weight ratios did not vary seasonally.) For computations of caloric requirements of loricariids, I assumed that resting metabolic rates were similar to those measured for four species of tropical fishes of similar size at similar temperatures in the laboratory (Kaysner and Heusner 1964), that active metabolism was three times resting metabolism (Kramer 1983), and that loricariids assimilated 20% of the organic matter produced in a given depth interval (see Power 1981 for details).

Estimates of periphyton production and of metabolic needs of loricariids within various depth intervals (fig. 22.5) suggest that loricariids in water deeper than 20 cm were food-limited at all times of year except during the early part of the rainy season (late April–June). During the late rainy season (July–November), algal production just met loricariid needs, except in water >40 cm deep. In the dry season, (December–early April) loricariid metabolic needs exceeded algal production except in very shallow water. These results are congruent with seasonal patterns of somatic growth rates in 4- to 9-cm long *Ancistrus*, which (as discussed above) peaked in the early rainy season, declined through the late rainy season, and stopped in the dry season.

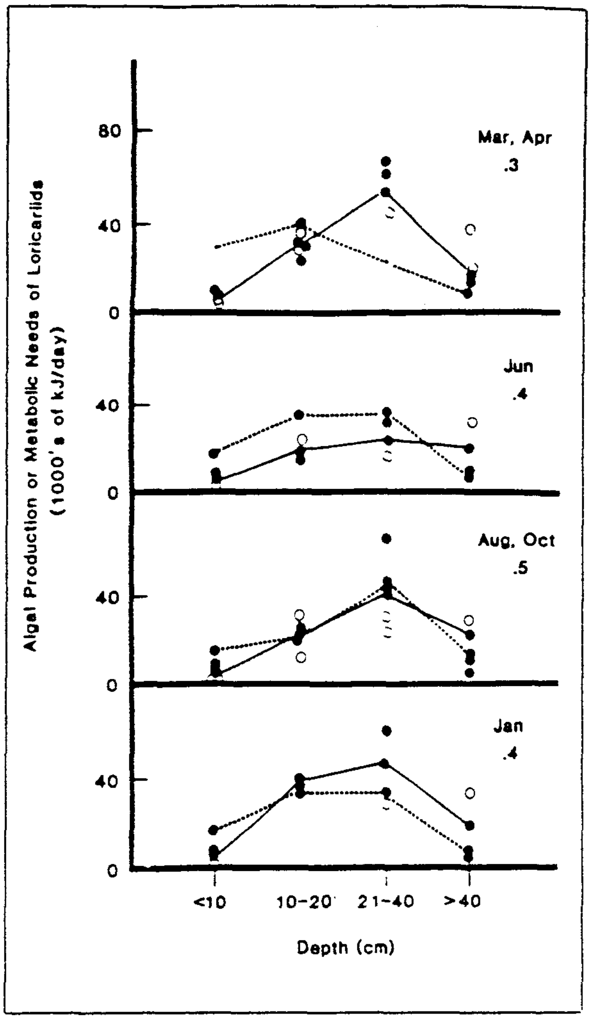

Figure 22.5. *Estimated harvestable periphyton production (*dotted lines*) and metabolic needs of loricariids grazing by day (*open circles*) and by night (*solid circles*) (*solid lines drawn through mean 24-hour requirements*) in four depth intervals during low (March, April), intermediate (January, June) and high (August, October) flow periods.*

In summary, three lines of evidence suggest that Rio Frijoles loricariids become increasingly food-limited with size and their shift to deeper water: steep depth gradients in algal standing crops; growth rates of loricariids; and comparisons of estimated depth-specific food renewal and collective metabolic needs of loricariids. Young fish in riffles are relatively safe from larger fish, their most important potential predators, but are limited, perhaps by bird predation, at densities below those necessary to deplete shallow algal standing crops. They may occupy shallows to avoid predatory fish, to exploit higher densities of food, or for both reasons. As catfish outgrow cover in shallow water and swimming predators in deeper water, they move down into pools where they are safe from wading and diving predators but where food is in short supply for much of the year. Large loricariids did not, over the range of food limitation I observed during a 28-month field study, compromise their safety by foraging in shallower water even when food was most limiting in the late dry season. As a result, mortality rates of large *Ancistrus* showed no seasonal variation, in contrast to the strong seasonal differences in rates of their somatic growth (Power 1984a).

Armored catfish that were experimentally starved for 8 and 18 days in their home pools were similarly conservative in their risk-taking behavior. After being released, starved fish showed no tendency to forage in shallower water than they had before starvation, or than was shown by fed control fish. Starved individuals did, however, spend more time out foraging on bedrock substrates in deep areas of pools that did fed controls (Power, Dudley, and Cooper, unpublished data). Some level of hunger might cause armored catfish to compromise their safety by foraging in shallow water. However, under the range of natural and experimental conditions that I have observed, predators increase food limitation for large armored catfish by excluding them from productive shallow areas of streams. Wading and diving predators therefore may intensify both intra- and interspecific competition for food, at least in the short term.

INTERSPECIFIC DIFFERENCES (COVER AND CRYPTICITY)

Differences in conspicuousness, and therefore perhaps in vulnerabilities to predators, occur among species as well as among size classes of grazing fishes. In the Rio Frijoles, *Ancistrus spinosus*, a stocky, spiny loricariid that outgrows most swimming predators, is common in deep (> 40 cm) pools with cover such as root tangles or undercut bedrock. In shallower pools that are relatively devoid of cover, *Ancistrus* is frequently outnumbered by a thin, cryptic species, *Rineloricaria uracantha*. When I tied a raft of small logs to the side of a pool 40 to 60 cm deep that formerly lacked cover, numbers of *Ancistrus* increased and those of *Rineloricaria* decreased over the following two weeks (fig. 22.6). Similar changes in *Rineloricaria* and *Ancistrus* numbers did not occur in a number of unmanipulated pools over the same time period. After cover addition and the influx of *Ancistrus*, *Rineloricaria* in the manipulated pool stopped using clay substrates in the deepest area, near the new shelter (fig. 22.7). Substrate use by *Ancistrus* was unchanged, except for their occurrence on the new wood of the raft. Replication, with observations of both species and of changes in algae, is needed to reveal whether interference or exploitative competition might change grazer guild composition after cover addition. Because behavioral interactions between *Ancistrus* and *Rineloricaria* were rarely observed even when the two species were in close proximity (Power 1984b), exploitative competition seems more likely than interference. These preliminary results are consistent with the hypothesis that

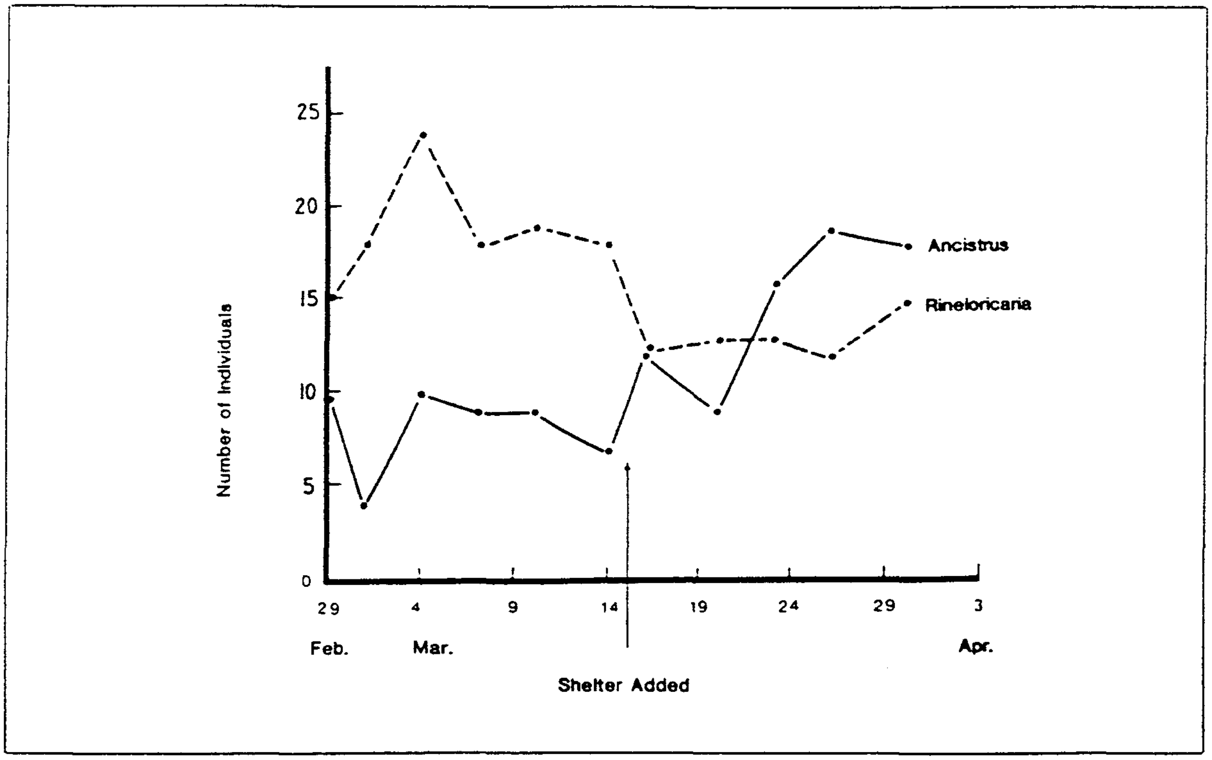

Figure 22.6. *Numbers of* Ancistrus *(solid line) and* Rineloricaria *(dashed line) counted in a sunny pool before and after the addition of a raft shelter.*

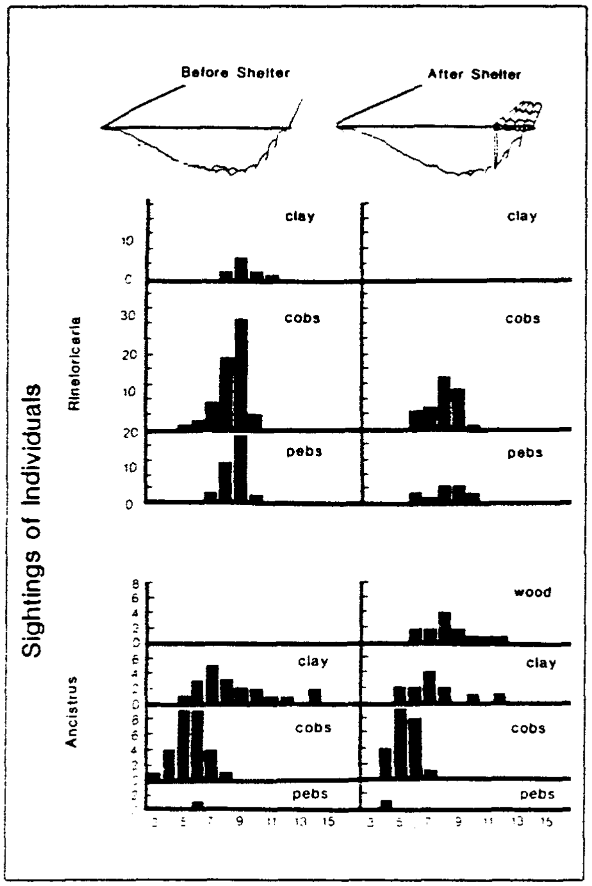

Figure 22.7. *Sightings of* Ancistrus *and* Rineloricaria *of various size classes on substrates in a sunny pool, before and after the addition of a raft shelter. Abscissa is standard length in centimeters.*

densities of *Ancistrus*, a potentially dominant competitor, can be limited by the availability of cover in sunny pools. When this limitation was relaxed, more *Ancistrus* colonized the pool, displacing *Rineloricaria*. If this interpretation is correct, it suggests a case in which predators create refuges from competition for subordinate competitors by making microhabitats too dangerous for dominant competitors to exploit. If predators promote coexistence of competing prey by altering their behavior rather than their relative numbers, the results may differ from patterns that arise from actual predation (Werner et al. 1983; Mittelbach, in press). Competition between prey species may be intensified or relaxed, depending on the degree to which one species will forage in areas avoided by the other.

DISCUSSION

Prey should avoid their most important predators or, if predictable, the areas where those predators forage most frequently and effectively. Predictability of the spatial distribution of risk depends on local abundances of various predators, on their behavioral flexibility, and on prey vulnerability. All three conditions change over long and short time scales. Prey may respond to changing risks in their habitats with learned or evolved changes in their behavior (Seghers 1974a, 1974b; Stein and Magnuson 1976; Stein 1979; Sih, this volume).

Spatial distribution of risk for stream fish is predictable when and where predators are jointly constrained by stream depth and prey size. Although common predators in streams such as bass (Savino and Stein 1982) and herons (Kushlan 1976, 1978; Meyerriecks 1962) are capable of a variety of hunting tactics, they are usually morphologically constrained to hunt most profitably while either wading, diving, or swimming. Each of these three hunting modes is effective only within certain parts of the stream channel (fig. 22.8).

Wading predators (e.g., raccoons, herons, and egrets) fish shallow areas along stream margins. Wading birds typically fish water no deeper than their leg lengths (Whitfield and Cyrus 1978; Kushlan 1978). Of 31 feeding behaviors used by 21 species of herons to catch aquatic prey, most (22 out of 31) are used in shallow water (Kushlan 1978). Wading depths for the little blue heron (*Egretta caerulea*) in a Panamanian stream ranged from 3 to 20 cm, with a mean of 11 (*N* = 15) (Power 1984a and unpublished data). Of nine species of wading birds in a South African lake, five fed in water < 10 cm deep, three fed in 20 cm or less, and one was seen feeding in water < 20 cm deep 85% of the time and in < 30 cm for the remainder (Whitfield and Cyrus 1978). In Ozark streams, green herons (*Buturoides striatus*) stood or walked along stream margins 90 to 95% of the time they were observed (Kaiser 1982). Mean foraging depths for adult herons were 30 cm (*N* = 36; range, 3–190 cm) and for juveniles, 8 cm (*N* = 8; range, 4–23 cm). The relatively high mean foraging depth for adults includes one observation of a heron jumping into water almost 2 m deep. Without this observation, mean foraging depth for adults would be 25 cm. Energetic feeding modes, such as plunging or diving into the water, are infrequently used by wading birds (Kushlan 1978). Although surprise may enhance the effectiveness of unusual hunting tactics, their infrequency and the awkwardness of a

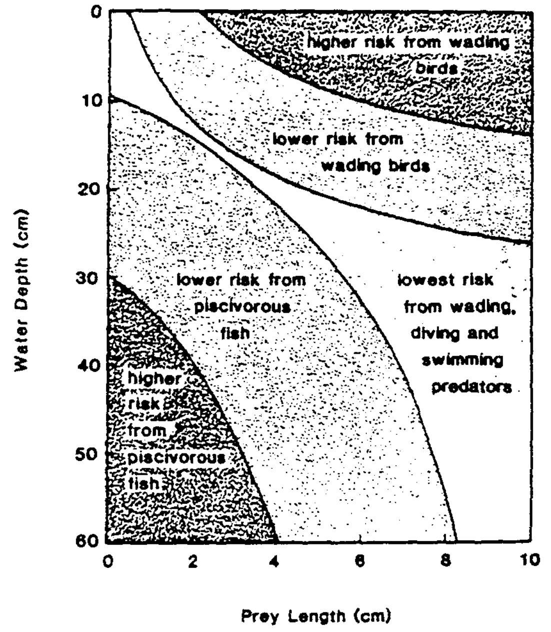

Figure 22.8. *Hypothesized distribution of depth- and size-specific risk for fish from swimming (e.g., fish) versus wading (e.g., herons) predators. Lines indicate "contours" along gradients of risk (adopted from Connell 1975, fig. 2-5). Quantitative limits for "Small and Large," "Deep and Shallow" are suggested for fishes and microhabitats in small (1st to 3rd order) streams.*

predator performing in defiance of its design constraints probably minimize their importance for potential prey. A laboratory study has shown that heron fishing effectiveness decreases with water depth. Capture success of a green heron fishing into a laboratory aquarium was 1.3 to 3.8 times higher when the bird fished within 10 cm of the water surface than when it fished at 10 to 20 cm or 20 to 30 cm, respectively (Kramer et al. 1983). These authors reason that near the surface birds can locate fish more precisely, there is less water resistance to slow the strike, and fish have less escape time after strike initiation. It therefore seems that although fish in deeper water are not completely free from attack by wading predators such as birds, their risk from such predators is much reduced with depth.

Diving predators such as kingfishers and skimming predators such as fishing bats fish near the water surface (Whitfield and Blaber 1978; Salyer and Lagler 1949). Kingfishers often initiate dives from perches but also will dive after hovering (Skutch 1957; Betts and Betts 1977; Junor 1972; Whitfield and Blaber 1978; Boag 1982), thereby gaining access to surface waters away from shore. The European kingfisher (*Alcedo atthis*, whose diet is more than 95% fish) usually does not dive into water deeper than 20 to 25 cm (Boag 1982). In an experimental pool, European kingfishers readily dove into water 2 to 22 cm deep, using their wings and chests to brake when they took fish from very shallow water (Boag 1982). Green kingfishers (*Chloroceryle americana*) were observed on 10 dives into points where a Panamanian stream was 8, 8, 8, 10, 11, 12, 12, 17, 40, and 43 cm deep. On the 43-cm dive, the kingfisher skimmed the water surface; depth in the water column where the bird fished on the 40-cm dive is not known (Power 1984a and unpublished data). Fishing bats of the Neotropics (*Noctilio leporinus*) skim and dip into streams, taking fish that rest at night in a quiescent state just beneath the water surface (Bloedel 1955). Australian bats known to fish (*Myotes vivesci*, *M. adversus*) have similar foraging methods (E. Pierson, personal communication). In laboratory experiments, *Noctilio* could not detect food a few millimeters below the surface but readily dipped at water upwellings or minute wires extending just above the water surface (Suthers 1965). Bloedel (1955) believed that bats did not pursue identified fish, but rather skimmed and dipped over stream regions they had learned were profitable hunting grounds.

Therefore, a variety of predators fishing streams have depth-limited access to prey. How big are the prey they can take? Wading predators and some diving predators can capture and consume larger prey than can most swimming predators in streams. These land-based predators are often large relative to animals that live within stream channels. In addition, many wading and diving predators can manipulate their prey and, if it is too large to swallow whole, consume it piecemeal. Manipulative abilities of raccoons are legendary. All heron species can handle and subdue prey too large to swallow whole: "Large, hard, or dangerous prey may be battered, rubbed, shaken, dropped or stabbed, and may be picked apart and eaten in pieces" (Kushlan 1978, p. 254). Kaiser (1982) observed green herons dragging large prey away from the stream (making escape less probable), breaking off spines, and consuming fish in pieces. Bats also can consume prey piecemeal, and some carnivorous species (*Vampyrum spectrum*) have carried 150-g prey (almost as big as themselves) back to roosts (Vehrencamp et al. 1977). Kingfishers have less ability to manipulate prey, and small species, such as pigmy kingfishers (*Chloroceryle aenea*) may be limited in the size of prey they can take. At least three kingfisher species, however, can handle fish at least as long as half their own body lengths. European kingfishers 16.5 to 18.5 cm long swallowed fish up to 8 cm long (Boag 1982). Belted kingfishers [*Ceryle alcyon*, 28 to 37 cm long (Udvardy 1977)] took trout 5 to 13.5 cm long from a Michigan river (Alexander 1979) and trout up to 17.8 cm long from other freshwater habitats in Michigan (Salyer and Lagler 1949). A ringed kingfisher [*Ceryle torquata*, 40 cm long (MacArthur 1972)] captured a 25-cm-long cichlid (*Geophagus crassilabrus*) in a Panamanian stream and subdued it by beating it against a large branch on which it perched (Power 1981).

Larger fish may be more vulnerable to wading and diving predators than smaller fish. They are inherently more conspicuous and less able to hide within small cover such as interstices of cobbles in riffles. In addition, larger prey may be preferred by large predators such as ringed kingfishers (MacArthur 1972), gray herons (*Ardea cinerea*) and little egrets (*Egretta garzetta*) (Britton and Moser 1982), and wood storks (Kushlan 1978). Fish flee the site of bird strikes, and local behavioral depression (Charnov et al. 1976) may make it advantageous for fishing birds to select larger prey. Great blue herons fishing a Michigan river ate trout from 7.6 to 33 cm long but appeared to select those from 18 to 30.5 cm long (Alexander 1979). Stoneroller minnows (*Campostoma anomalum*) dominated fish remains in belted kingfisher nests, and dace (*Rhinichthys* spp.) were rare, despite the greater abundance of dace in a New York stream (Eipper 1956). The kingfishers may have selected the larger stonerollers over the small dace (Eipper 1956). In addition, stonerollers were breeding in shallow water while kingfishers were nesting, and may have been particularly available. [Although kingfishers increase the size of fish brought to nestlings as they grow (Skutch 1957; White 1938), wading birds do not select small prey for their young, but instead deliver well-digested food (Kushlan 1978).] Finally, large or wide fish may be less likely to escape after capture by thin-billed herons, which tend to grasp small or thin fish but stab and seriously wound larger prey (Recher and Recher 1969b; Kushlan 1978).

For the reasons outlined above, it would be very difficult for prey in streams to "escape in size" from wading and some diving predators. Prey might, however, outgrow vulnerability to swimming predators, which must live or at least maneuver within stream channels and are therefore limited in body size. Moreover, piscivorous fish, the most common swimming predators in many streams, have limited ability to manipulate prey after capture and in most cases must swallow them whole (Popova 1978; Hyatt 1979). The length of prey many predatory fish can take varies linearly with their own body lengths. Maximum prey size found in predator guts is usually 30 to 50% as long as the predator; average prey size ranges from 10 to 20% of the predator's length, whereas minimum prey size does not vary systematically with predator length and is usually < 10% of it (table 22.3). Although larger predatory fishes can take larger size ranges of prey, they do not always eat the largest prey available, as handling time constraints may make smaller prey more profitable (Werner 1974, 1977; Hyatt 1979). Several small fish are digested more rapidly than one large fish, especially if larger prey have dense scaly armor or rigid skeletons (Popova 1978). Stream fish, particularly those like loricariid catfish with spines and armor that enhance their effective size, may outgrow vulnerability to "gape-limited" (Zaret 1980) swimming predators.

In contrast to wading and diving predators, many swimming predators [such as piscivorous fish and otters but not watersnakes (Mushinski et al. 1982)] fish primarily in deeper parts of streams. Piscivorous fish may hunt most commonly in deep water to avoid wading and diving predators themselves, or because they have more room to maneuver in deeper areas, or for clearer reception of pressure signals along their lateral lines (Clark Hubbs, personal communication). In six New Zealand rivers, adult brown trout (32–55 cm fork length) were observed feeding in depth from 14 to 122 cm, with frequency of sightings increasing sharply at depths ≥ 40 cm. The preferred feeding depth was estimated to be 65 cm (Shirvell and Dungey 1983). In a Michigan lake, 97% of bass counted

Table 22.3. *Linear regressions of prey length (Y) versus predator length (X)*

Predator	Maximum prey	Average prey	Minimum prey	Source
Esox lucius, pike, 4–75 cm	$Y = 0.51X + 0.13$ $r = .99$ $N = 9$	$Y = 0.11X + 1.73$ $r = .93$ $N = 9$	$Y = 0.005X + 2.37$ $r = .16$ $N = 9$	(1)
Silurus glanis, sheatfish, 5–100 cm	$Y = 0.41X - 0.13$ $r = .98$ $N = 9$	$Y = 0.09X + 1.96$ $r = .93$ $N = 9$	$Y = 0.0002X + 2.10$ $r = .02$ $N = 9$	(1)
Perca fluviatilis, perch, 3–41 cm	$Y = 0.41X + 5.47$ $r = .52$ $N = 8$	$Y = 0.27X - 0.09$ $r = .97$ $N = 8$	$Y = 0.07X + 0.42$ $r = .85$ $N = 8$	(1)
Stizostedion lucioperca, zander, 4–70 cm	$Y = 0.35X + 1.00$ $r = .95$ $N = 9$	$Y = 0.17X + 0.97$ $r = .98$ $N = 9$	$Y = 0.04X + 0.70$ $r = .71$ $N = 9$	(1)
Aspius aspius, asp, 6–57 cm	$Y = 0.34X + 0.56$ $r = .96$ $N = 7$	$Y = 0.09X + 0.62$ $r = .95$ $N = 7$	$Y = 0.01X + 0.34$ $r = .73$ $N = 7$	(1)
Stizostedion vitreum, walleye, 11–23 cm	$Y = 0.53X - 1.90$ $r = .98$ $N = 4$	$Y = 0.29X - 0.88$ $r = .63$ $N = 44$	$Y = 0.15X - 0.29$ $r = .95$ $N = 7$	(2)
Pomoxis annularis, white crappie, 17–32 cm	$Y = 0.44X - 11.51$ $r = 0.94$ $N = 6$	$Y = 0.30X + 3.62$ $r = .81$ $N = 7$	$Y = 0.13X + 12.75$ $r = .54$ $N = 6$	(3)

Sources: (1) Popova 1978, Fig. 9.6; (2) Forsythe and Wrenn 1979; (3) Burris 1956, cited in Carlander 1977b.

in snorkeling censuses were in water > 30 cm deep, and 91% were in > 50 cm deep (Werner 1977). Depths in which predatory fish will forage may change with hunger, experience, light, season, cover, or other factors, but I know of no field data examining these relationships.

Stream fish may cross riffles shallower than areas where they would linger. Although movements of bass and trout through natural stream reaches have been studied (Gerking 1959; Larimore 1952; Fajen 1962), data on depths of intervening riffles at the time of pool-to-pool movements are not, to my knowledge, available. Such behavioral data would be useful in predicting flow conditions that would permit the coexistence of predatory fishes and their prey in streams with semi-isolated pools, like Brier Creek (Power et al. 1985).

The bigger-deeper distribution is one pattern predicted for prey that avoid predators subject to the size and depth constraints described above. Different predators could produce different patterns in prey assemblages. Watersnakes (*Nerodia* spp.) are "gape-limited" predators that forage in shallow as well as deep water (Mushinkski et al. 1982). Mergansers (*Mergus* spp.) pursue fish underwater in areas up to several meters deep (Lindroth and Bergstrom 1959). They are capable of swallowing large fish in a gradual, snakelike fashion. One merganser disgorged a trout 37 cm long (Salyer and Lagler 1949). White (1957) found suckers 28 cm long and an eel 41 cm long in merganser stomachs. It would be interesting to study the depth distributions of fish in habitats such as the Margaree River of Nova Scotia where these ducks are important predators (White 1936, 1939). Various crocodilians and otters are other swimming predators capable of taking large fish in streams. These predators may once have been important in many streams where they are now rare or absent because of human hunting and habitat destruction.

One of the few quantitative studies of the relative importance of various predators in streams was conducted in a managed trout stream in Michigan. Alexander (1979) estimated numbers and per capita feeding rates of four swimming predators [large brown trout (*Salmo trutta*), mergansers, mink, and otters]: one diving predator (belted kingfisher) and one wading predator (great blue heron) in a 32-km reach of the Au Sable River. Herons and large brown trout were the most important predators, taking, respectively, 19 to 20% and 12 to 24% of the annual trout production not caught by fishermen. American mergansers, belted kingfishers, mink, and otter each took

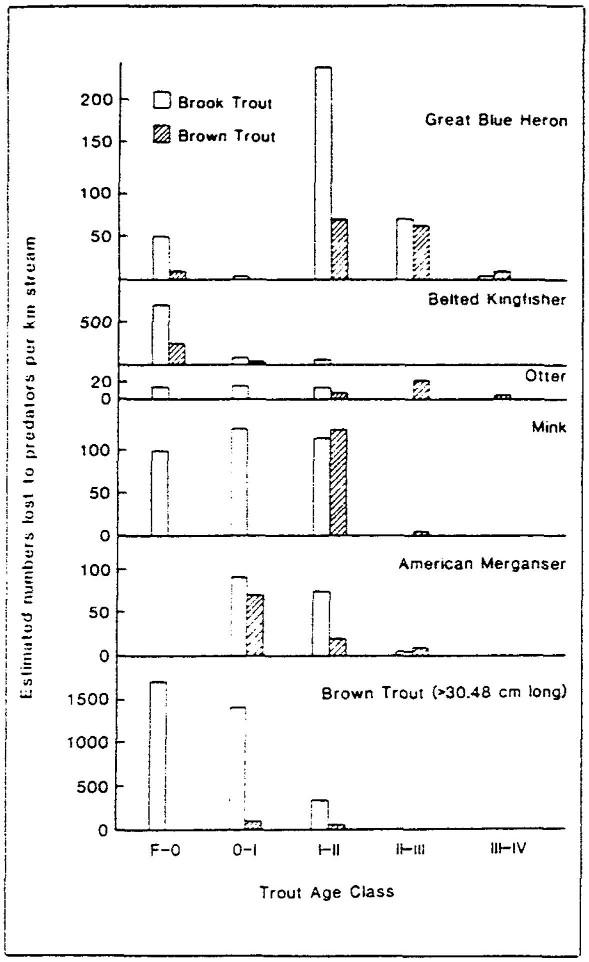

Figure 22.9. *Numbers of brook and brown trout of various age classes lost to predators. Data from tables 2-5 in Alexander 1979. Numbers of trout lost from two stream reaches subject to different angling regulations have been averaged. For given age classes, ranges of lengths (total or fork length in millimeters) reported by Carlander 1977a for North American brook trout are: F-O: < 15; O-I: 15-236; I-II: 56-292; II-III: 66-343; and III-IV: 102-419. For brown trout, these lengths are: F-O: <25; O-I: 25-198; I-II: 64-241; II-III: 132-366; III-IV: 157-495.*

< 10% of this production (computed from Alexander 1979: table 8). Herons, the most important wading predators, took larger size classes of trout, and brown trout, the most important swimming predator, took small brook trout (*Salvelinus fontinalis*) (fig. 22.9). In the Au Sable River in its contemporary managed condition, then, fish avoiding their two most important natural predators would maintain bigger–deeper distributions.

Stream fish distributions, their vulnerability to predators, and their access to food are affected by other physical factors that are not independent of depth in streams: in particular, current, cover, substrate, and surface rippling (e.g., Moyle et al. 1982; Binns and Eiserman 1979; Burns 1971; Jenkins 1969; Gibson 1966). Hypotheses I have presented are clearly oversimplifications of interactions of physical and biotic factors in stream communities. Nevertheless, quantitative and experimental studies of the relationships between depth, size, and predation risk for stream fish are likely to be of basic and applied interest. Depth is an easily measured and manipulated habitat variable that appears to affect space use by stream fish, and hence the carrying capacities of streams for their populations. Quantitative data on depth-specific foraging frequencies and size selectivities of predators on stream fish, and experimental tests of hypotheses regarding the extent and consequences of predator avoidance by particular classes of stream fish, should prove useful in explaining and predicting the dynamics and effects of fish populations in streams with different, and differing, flow regimes.

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