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**Title**

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**Permalink**

https://escholarship.org/uc/item/09q2q691

**Journal**

Environmental Biology of Fishes, 26(4)

**ISSN**

0378-1909

**Authors**

Power, Mary E

Dudley, Tom L

Cooper, Scott D

**Publication Date**

1989-12-01

**DOI**

10.1007/bf00002465

Peer reviewed

# Grazing catfish, fishing birds, and attached algae in a Panamanian stream

Mary E. Power[1], Tom L. Dudley[2] & Scott D. Cooper[2]
[1] *Department of Zoology, University of California, Berkeley, Berkeley, CA 94720, U.S.A.*
[2] *Department of Biological Sciences, University of California, Santa Barbara,*
*Santa Barbara, CA 93616, U.S.A.*

## Synopsis

In streams where algivorous fishes abound, striking variation of attached algae often develops along depth gradients, with bands of high standing crops in shallow water (<20 cm) and sparse standing crops on deeper substrates. Experimental results from a stream in central Panama support the hypothesis that vertical variation in algal standing crops arises when grazing fishes avoid predators in shallow water by forgoing food resources that accumulate there. When 38 rocks bearing algae in a stream in central Panama were transferred from shallow (<20 cm) to deeper (>20 cm) water, algae were rapidly consumed by grazing catfish. Catfish were removed from three stream pools and left in place in three control pools. Ten days after catfish removal, algal standing crops in deep and shallow areas of removal pools were similar, while algal standing crops were higher in shallow than in deep areas of control pools. Catfish were exposed to fishing birds in open-topped enclosures. In one of three series of these pens, most catfish in shallow pens (10 and 20 cm) disappeared after 14 days, while catfish in deeper pens (30 and 50 cm) did not. Other groups of catfish which were caged 8 days showed differences in behavior depending on whether they had been fed or starved. After their release into their home pool, starved catfish spent more time feeding than did fed catfish. Despite their apparently increased hunger levels, starved catfish did not venture into shallow water to obtain algae. These results support the view that predator induced avoidance by grazers of certain areas can produce spatial pattern in the flora of flowing water communities.

## Introduction

By restricting the foraging area of their prey, predators can create spatial refugia for organisms on which their prey feed. Multi-trophic level effects of predators via their sublethal influences on prey behavior have been found in a growing number of freshwater habitats (Schlosser 1987, 1988, Mittelbach 1984, Gilliam & Fraser 1987, Holomuzki 1986, Power 1987, Kerfoot & Sih 1987). Distributions of attached algae often clearly indicate spatial variation in herbivory, which may arise from predator avoidance by grazers, or from other factors (Hay 1981, 1984, Sammarco 1982, Power 1983, Power et al. 1985, Lubchenco 1978, and many others). We investigated the role of predator avoidance by grazers in establishing vertical gradients in algal standing crops that are widespread in streams populated by grazing fishes.

In tropical and temperate streams with high densities of grazing fishes, bands of algae often develop along shallow margins, but algal abundance drops

off steeply when depths exceed 15–25 cm. This depth corresponds to the maximum depths at which wading and diving birds feed most frequently and effectively (Whitfield & Cyrus 1978, Boag 1982, Kramer et al. 1983, Power 1984a, 1987). Bands of algae along stream margins have been observed in streams in Panama (Power 1984a) and Trinidad (J.A. Endler, personal communication) inhabited by grazing catfishes (Loricariidae), and in streams in Oklahoma with dense populations of grazing minnows, Campostoma anomalum (Power & Matthews 1983). Here we report results from a series of simple experiments that tested three hypotheses:

H(1): Grazing by catfish limits algal depth distributions. Predictions: Algal abundance will decrease as catfish densities increase with depth; in pools from which catfish are removed, algal densities will be more similar on deep and shallow substrates.

H(2): Predation hazard, primarily from fishing birds, constrains catfish depth distributions. Predictions: Catfish will avoid water shallower than 20 cm, where birds fish frequently and effectively. Catfish confined in shallow water will disappear faster than catfish confined in deeper water.

H(3): Catfish will take risks if rewards are sufficient. Prediction: Catfish will graze in shallow water, where algal standing crops are high, when sufficiently hungry.

## Study site

The Rio Frijoles is a clear stream that flows over marine sedimentary rocks and metamorphic basalts in the Parque Nacional Soberania of central Panama (9°9' N, 79°44' W). Baseflow discharge varies from $0.5 \, \text{m}^3 \, \text{s}^{-1}$ in the rainy season to $0.1 \, \text{m}^3 \, \text{s}^{-1}$ in the dry season (Power 1981). Most of the stream's watershed lies within mature second growth forest; only short reaches of some headwaters lie within land that is presently cleared. In reaches underlain by soft sedimentary marine deposits, the stream maintains a wide floodplain, forest canopy is >25% open (Power 1984b), and

much sunlight reaches the bed. Where the river runs through more resistant basalts, channel walls are steep and stable, forest grows to the edge of the stream, and canopies <25% open shade the bed.

The Rio Frijoles supports dense populations of three species of algae-grazing loricariid catfish: Rineloricaria uracantha Kner & Steindachner, Ancistrus spinosus (Eigenmann & Eigenmann) and Hypostomus plecostomus (Linnaeus). A fourth species, Chaetostoma fischeri Steindachner, is less common and occurs primarily where deep, fast flowing habitat is available (Power 1981, J.D. McPhail, D.L. Kramer, G.E.E. Moodie, unpublished data).

Armored catfish in the Rio Frijoles graze almost entirely on periphyton on hard substrates: bedrock, boulders, cobbles, and large pieces of submerged wood. They are the only major grazers of attached algae in deeper stream habitats (Power 1981), where invertebrate grazers appear to be limited by high densities of predatory fishes. During an intensive 28 months field study from 1978 to 1980, algal standing crops were very scant on substrates that were deeper than 20 cm, but relatively large standing crops of algae, including filamentous bluegreens, occurred in shallower habitats along stream margins (Power 1984a). In March of 1985, when we carried out experiments reported here, algal standing crops were also generally higher in shallow water.

## Methods and results

*Algal transfers.* We tested the hypotheses that algae in shallow water were unpalatable, or that they accumulated too rapidly to be controlled by grazers, by transferring 38 algal-covered cobbles from shallow to deep water. Grazing catfish removed all conspicuous algae from these substrates within hours, and sometimes within minutes, showing that the food was acceptable, and that catfish could easily have depleted periphyton in shallow water had they fed there.

*Effect of depth on disappearance of loricariids from open-topped pens.* The most common piscivorous

birds sighted along the Rio Frijoles were mature and immature little blue heron, *Egretta caerulea,* green kingfishers, *Chloroceryle americana,* and night-fishing rufescent tiger herons, *Tigrisoma lineatus.* Birds observed fishing during the 1978–80 study (Power 1984b) and the 1985 study reported here generally foraged in water <20 cm deep (in 27 out of 28 observations where depth of fishing was measured).

To examine the vulnerability of armored catfish at various depths to predators, we enclosed fish in open-topped pens that were similar in area (1 m²) and substrate (gravel <45 mm median diameter), but were set in 10, 20, 30 and 50 cm of water. Pens were made of black plastic screen (6.4 mm mesh) supported by four 2.54 cm diameter PVC pipes. The tops of pen walls projected about 10 cm above the water surface. Four pens (one at each depth) were installed in each of three reaches of stream where we had previously seen little blue herons fishing. We stocked each pen with size-matched groups of the two most common species of loricariids: *Rineloricaria uracantha,* a thin cryptic species abundant in deeper riffles and in heads, tails and margins of pools, and *Ancistrus spinosus,* the most common species in deeper stream pools (Fig. 1). After twelve days, catfish remaining in pens were counted.

In one of the series of four pens, most *R. uracantha* had disappeared from pens in 10 and 20 cm of water, but the majority remained in the 30 and 50 cm deep pens (Fig. 2). Roughly half of the *A. spinosus* were also missing from the 10 and 20 cm pens, and most were still present in pens that were 30 and 50 cm deep (Fig. 3). We did not witness predation, but saw both little blue herons and green kingfishers within one meter of the shallow cages in this series of pens on several occasions.

At the other two stream reaches, all catfish remained in all the pens when experiments were terminated after twelve days of exposure. We do not have sufficient information to evaluate whether site differences or simply the short duration of the experiment accounted for the lack of predation at these other two reaches.
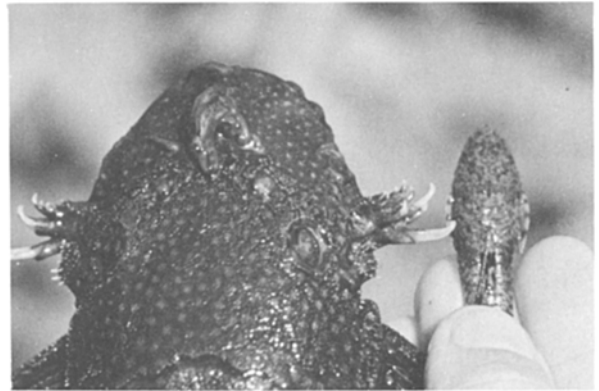


*Fig. 1. Ancistrus spinosus* and *Rineloricaria uracantha,* the two most common loricariid catfish in the Rio Frijoles.

*Effect of loricariid removal on attached algae in pools.* Three pairs of pools, one sunlit, one half shaded, and one darkly shaded, were selected. Paired pools were physically similar and close or adjacent along the reach (Table 1). Loricariids were counted in pools by a snorkeller (MEP) who
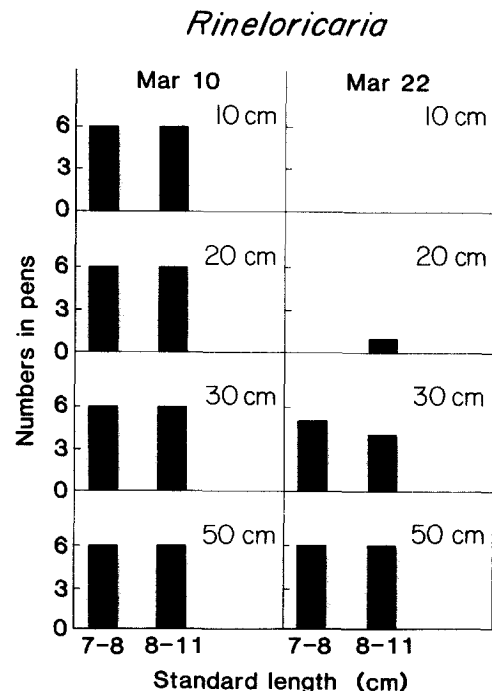


*Fig. 2.* Numbers of *R. uracantha* stocked on March 10 and remaining on March 22 in open-topped enclosures at four water depths.
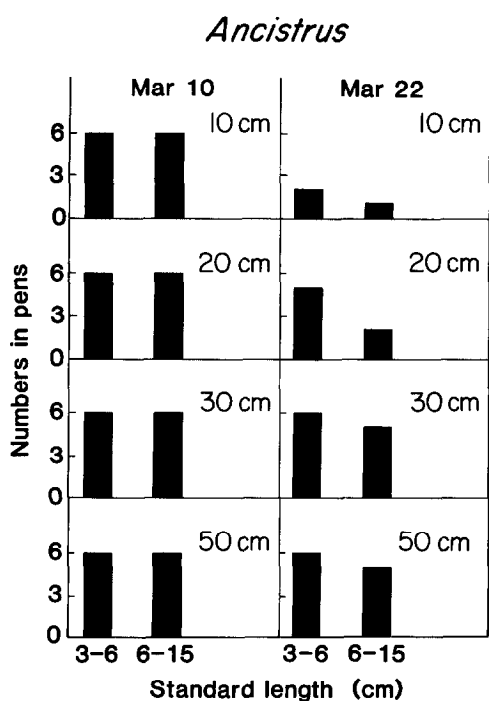
## Ancistrus



Fig. 3. Numbers of A. spinosus stocked on March 10 and remaining on March 22 in open-topped enclosures at four water depths.

recorded numbers and the estimated lengths of each species. One pool from each pair was selected by coin toss for loricariid removal. Fish were netted by snorkellers using aquarium net frames fitted with monofilament gill net, a capture technique that only minimally disturbed the habitat. Over a 6 d period, we removed sufficient numbers of loricariids from these pools to depress their numbers (Table 2). In removal pools, the numbers of catfish, particularly of R. uracantha, that were removed often exceeded those previously counted. This may be due to immigration of fish to pools during the removal period, as pools were adjoined by deep riffles which provided habitat for small loricariids and passage for all size classes. In addition, resident R. uracantha may have been overlooked during counts, as they are extremely cryptic when quiet and half-buried in sand. The smallest of the four species, R. uracantha has lower grazing rates (as estimated by area covered per individual per time) than the larger loricariid species (Power 1984b).

Before removal, and 10 and 17 d after removal, algae were collected from substrates above and below the 20 cm depth contour in each pool. With an aspirator fitted with a glass intake nozzle, we simultaneously scraped and aspirated algae from known areas, using a flexible template pressed to the substrate. Algae were preserved in 1–3% Lugol's solution, and later examined under 400× and

Table 1. Characteristics of paired pools in loricariid removal experiments.

| Pool | Length (m) | Max. width (m) | Area* (m²) | Max. depth (cm) | Canopy (% open) | Substrate |
|---|---|---|---|---|---|---|
| Otter Scat (control) | 39.0 | 9.4 | 288 | 100 | 10–25 upstream <10 downstream | basalt bedrock |
| Pyralid (removal) | 22.1 | 4.9 | 85 | 97 | <10 | basalt bedrock |
| Lower Polistes (control) | 32.0 | 5.2 | 131 | 74 | 25–50 | bedrock cobbles |
| Upper Polistes (removal) | 22.9 | 4.2 | 76 | 76 | 25–50 | bedrock cobbles |
| Cecropia (control) | 12.7 | 4.2 | 42 | 45 | >50 | cobbles clay |
| Blue Clay (removal) | 9.7 | 5.5 | 42 | 55 | >50 | cobbles clay |

* Plan view area estimated by assuming pools are elliptical in shape.

weighed in the laboratory. Preserved samples were dried to constant weight at 80°C, weighed, combusted 1 h at 510°C, and re-weighed for determination of ash-free dry weight.

Unfortunately, most algal samples were lost in transit between Panama and California. Too few samples were available to compare algal standing crops in the two sunny pools on any date, or in the other pools before loricariid removals, or 17 d afterwards. Sufficient samples were available to compare algal biomass in the dark and half-shaded pools 10 d after loricariid removals. Algal standing crops in control pools were 4–20 times higher in shallow than in deep areas, whereas algal standing crops in removal pools were similar in shallow and deep areas (Table 3). Using the mean algal biomass for deep and shallow areas of each of the four pools as replicates (two depths × four pools = eight values), we performed a two-way ANOVA examining the effects of treatment and depth, and their interaction, on algal standing crops. Main effects of treatment and depth on algal biomass were not significant (F = 2.4 and 0.2, p = 0.19 and 0.70, df = 1 and 1, respectively). The interaction of depth and treatment, however, could account for a significant amount of the variation in algal biomass (F = 8.8, p = 0.04, df = 1). These results suggest that differences in algal standing crop between shallow and deep areas of pools were reduced by the removal of loricariids.

*Effect of food deprivation on loricariid behavior*

*and space use.* To examine the effect of hunger on the tendency of loricariids to forage in shallow water, we manipulated hunger levels of catfish from a single large pool with a dense catfish stock. Before the manipulation, the pool was mapped, and areas of hard bedrock substrate, and soft gravel, sand and detrital substrates were measured. In addition, we measured the area of stream bed under four depth intervals (Table 4). Markers were placed on the stream bed to delineate depth contours so that the loricariids occupying various substrates and depth intervals could be counted during bankside observations. Sitting on the bank, one of us (MEP) observed catfish grazing over a gridded bedrock platform marked off into squares 0.5 m on an edge. At 10–minute intervals from 1100 to 1140 h, the numbers and estimated lengths of various species and size classes of loricariids on the bedrock platform, and on areas of soft substrate, were recorded.

After these baseline observations, we caged two groups of closely size-matched loricariids captured from the mapped pool. Fifteen *R. uracantha* (SL range = 63–105 mm), 7 *A. spinosus* (50–123 mm) and 2 *H. plecostomus* (55–71 mm) were placed in each cage. Catfish were enclosed in large 1 m³ roofed cages (mesh size = 6.4 mm). One group was held without food; the other was fed on attached algae transferred from stream margins and on canned green beans. After the first three days of captivity, captive loricariids readily consumed both foods. Fed and starved groups were marked with

*Table 2.* Effect of loricariid removal on loricariid numbers in pools.

| Pool | Loricariids counted (before removal) | | | | Total No. m⁻² | Loricariids removed March 7–12 | | | | Loricariids counted (after removal) | | | | Total No. m⁻² |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | R* | A* | H* | C* | | R | A | H | C | R | A | H | C | |
| Otter Scat | 3 | 6 | 5 | 6 | 20 | 0.07 | 0 | 0 | 0 | 0 | 2 | 7 | 0 | 6 | 15 | 0.05 |
| Pyralid | 22 | 11 | 0 | 3 | 36 | 0.42 | 25 | 12 | 3 | 2 | 8 | 3 | 1 | 2 | 14 | 0.17 |
| Lower Polistes | 24 | 7 | 2 | 0 | 33 | 0.25 | 0 | 0 | 0 | 0 | 43 | 7 | 2 | 0 | 52 | 0.40 |
| Upper Polistes | 26 | 7 | 2 | 0 | 35 | 0.46 | 34 | 8 | 6 | 0 | 12 | 3 | 0 | 0 | 15 | 0.20 |
| Cecropia | 20 | 2 | 1 | 4 | 27 | 0.64 | 0 | 0 | 0 | 0 | 19 | 3 | 2 | 2 | 26 | 0.62 |
| Blue Clay | 22 | 13 | 1 | 1 | 37 | 0.88 | 55 | 13 | 4 | 2 | 3 | 1 | 1 | 0 | 5 | 0.12 |

* R = *Rineloricaria*, A = *Ancistrus*, H = *Hypostomus*, C = *Chaetostoma*

differently colored plastic beads attached with stainless-steel wire through the dorsal armor immediately in front of the first dorsal spine. After 8 d, both groups were released into their home pool (cages were opened, and fish allowed to swim out).

Before catfish were caged, they tended to actively feed on hard substrates, and to rest on soft substrates where they were less conspicuous (*Rineloricaria*) (Fig. 4) or under bedrock ledges, out of sight (*Ancistrus, Hypostomus*). After experimental manipulation of hunger, a greater proportion of the starved individuals sighted were on hard substrates and were feeding, relative to fed catfish or catfish observed before caging (Fig. 4). Fewer experimentally fed catfish were observed on platforms because replete *Ancistrus* and *Hypostomus* rested under ledges (out of sight). Fed and starved individuals were sighted during snorkelling censuses, showing that they had not emigrated from the pool. On
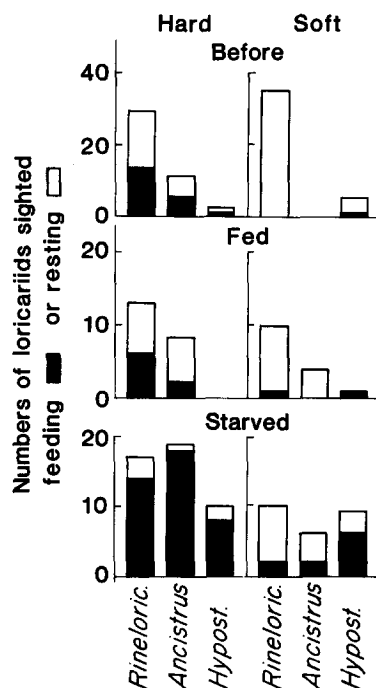


*Fig. 4.* Positions and behavior of loricariids before they were caged, and on the day of their release, after they were starved or fed in cages in their home pool. 'Hard substrate' is a bedrock platform; 'soft substrate' is gravel, sand, or detritus.

*Table 3.* Effect of loricariid removal on periphyton biomass in pools.

| Pool | Periphyton biomass (mg afdw cm$^{-2}$) | | | | | |
|---|---|---|---|---|---|---|
| | <20 cm depth | | | >20 cm depth | | |
| | mean | SE | (n) | mean | SE | (n) |
| Otter Scat (control) | 4.0 | 1.8 | (3) | 0.2 | 0.1 | (3) |
| Pyralid (removal) | 1.1 | 0.2 | (3) | 1.2 | 0.6 | (4) |
| Lower Polistes (control) | 2.4 | 0.8 | (4) | 0.6 | 0.5 | (3) |
| Upper Polistes (removal) | 1.4 | 0.6 | (4) | 0.8 | 0.3 | (3) |

*Table 4.* Area of hard and soft substrates in the hunger manipulation pool.

| Depth (cm) | Hard substrate (m$^2$) | Soft substrate (m$^2$) | Total (m$^2$) |
|---|---|---|---|
| <10 | 3.98 | 6.09 | 10.07 |
| 10–20 | 4.23 | 8.14 | 12.37 |
| 21–40 | 7.50 | 17.17 | 24.67 |
| >40 | 4.62 | 14.92 | 19.54 |
| Total | 20.33 | 46.32 | 66.65 |

each of 13 scan samples (Altmann 1974) made on the day of release, more starved than fed catfish were sighted on platforms, and more were feeding (Table 5). Larger proportions of starved than fed catfish, and of starved than unmarked catfish, were feeding when sighted during the 13 scan samples. Unmarked catfish, which had not been caged, were free to feed on natural substrates, and therefore were presumably less hungry than were caged fish that had been deprived of food. Of the uncaged and fed loricariids sighted on the bedrock platform, <26% were feeding, whereas over 75% of the starved fish that were observed were feeding (Table 5).

One potential source of dependence in these data is the influence of a fish's behavior during one scan on its own or another fish's behavior during the next scan. This potential dependence is reduced by the short duration of the behavioral states (resting, which usually lasted <30 s, and feeding,

which usually lasted <20 s) relative to the 10 min interval between scan samples. Another source of dependence could be time dependent changes in the probability of an individual's resting or feeding, for example, if fish satiated. However, there were no trends in the proportions of sighted starved or fed fish that were feeding or resting over the two hour observation period. Because these sources of dependence seemed minor, we performed median tests (Zar 1984) on proportions of fish sighted feeding vs. resting. The results (fed vs. starved: chi square = 6.04, p<0.025, df = 1; uncaged vs. starved: chi square = 7.58, p<0.01, df = 1) indicate that feeding activity, and presumably hunger level, was higher for starved catfish than for fed catfish or catfish that had not been caged.

Despite the apparent increase in hunger levels of starved catfish, they showed no increased tendency to venture into shallower areas (Fig. 5) to obtain higher standing crops of food. Only 2 out of 186 recorded sightings of loricariids were of individuals at depths of less than 20 cm, and these were of 3 cm long *A. spinosus* (smaller than most individuals in pool habitats) before caging.

The possibility that hunger would affect loricariid movement between pools was checked by a snor-

*Table 5*. Number of armored catfish that had been uncaged (U), or caged and starved (S) or fed (F) for eight days, sighted resting or feeding on the day of the latter's release.

| Time | Activity | Treatment | | | Probability (Fisher's Exact Test) | |
|------|----------|-----------|-----|---------|---------|-------------|
| | | uncaged | fed | starved | F vs. S | (U + F) vs. S |
| 1310 | feeding | 0 | 0 | 4 | 0.14 | 0.003 |
| | resting | 9 | 2 | 1 | | |
| 1320 | feeding | 1 | 0 | 1 | 0.60 | 0.02 |
| | resting | 8 | 2 | 2 | | |
| 1330 | feeding | 0 | 0 | 5 | 0.02 | 0.02 |
| | resting | 0 | 3 | 0 | | |
| 1340 | feeding | 0 | 1 | 5 | 0.50 | 0.001 |
| | resting | 11 | 1 | 2 | | |
| 1350 | feeding | 3 | 1 | 5 | 1.00 | 0.04 |
| | resting | 8 | 0 | 0 | | |
| 1400 | feeding | 5 | 1 | 3 | 0.34 | 0.15 |
| | resting | 10 | 2 | 1 | | |
| 1410 | feeding | 7 | 0 | 5 | 0.05 | 0.03 |
| | resting | 8 | 2 | 0 | | |
| 1420 | feeding | 8 | 1 | 5 | 0.86 | 0.38 |
| | resting | 5 | 0 | 1 | | |
| 1430 | feeding | 2 | 1 | 6 | 0.03 | 0.0004 |
| | resting | 14 | 3 | 0 | | |
| 1440 | feeding | 2 | 1 | 2 | 0.48 | 0.28 |
| | resting | 10 | 3 | 3 | | |
| 1450 | feeding | 1 | 0 | 3 | 0.42 | 0.06 |
| | resting | 13 | 2 | 4 | | |
| 1500 | feeding | 0 | 0 | 4 | 0.03 | 0.0003 |
| | resting | 12 | 3 | 0 | | |
| 1510 | feeding | 1 | 3 | 6 | 0.34 | 0.005 |
| | resting | 21 | 3 | 3 | | |
| mean | feeding | 2.3 | 0.7 | 4.5 | | |
| | resting | 9.9 | 2.0 | 1.3 | | |
| prop. | feeding | 0.18 | 0.26 | 0.78 | | |

Before    Starved    Fed

< 10 cm deep

10 - 20 cm deep

20 - 40 cm deep

< 40 cm deep

Numbers of sightings

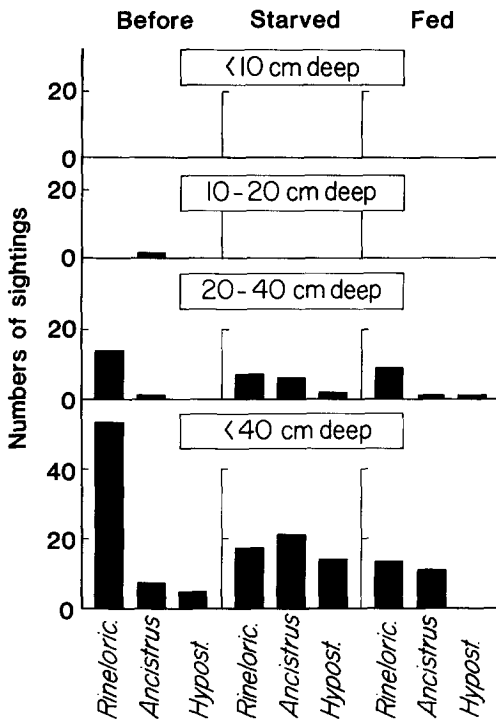Rineloric.  Ancistrus  Hypost.  Rineloric.  Ancistrus  Hypost.  Rineloric.  Ancistrus  Hypost.

*Fig. 5.* Sightings of loricariids in four depth intervals before enclosure, and after being fed or starved for eight days.

keller (MEP) who searched the three pools down-stream and three pools upstream from the experimental pool once daily for three days after caged fish were released. Only one marked individual (a 11 cm male *R. uracantha* which had been starved) was seen during these searches. He was three pools upstream from the home pool.

## Discussion

Predators in freshwater communities can restrict the foraging area of vertebrates (Cerri 1983, Helfman 1986, Holomuzki 1986, Werner et al. 1983, Schlosser 1988, Power & Matthews 1983, Power et al. 1985) and invertebrates (Stein 1979, Stein & Magnuson 1976, Cooper 1984, Sih 1982). Sublethal effects of predators on prey can have repercussions for individual prey fitness (Cooper 1984, Sih 1982), for prey population dynamics (Mittelbach & Chesson 1987, Dill 1987), and for interactions with other

species (Jeffries & Lawton, Abrams 1984, Mittelbach 1986, 1988, Kerfoot & Sih 1987). Community-level consequences are particularly conspicuous when predators restrict foraging areas of grazers that consume sessile, rapidly growing foods like attached algae (Hay et al. 1983, Power et al. 1985).

How predictable are the areas in which algae enjoy spatial escapes from herbivory? Predation hazard in a given area may change (e.g., if predators leave the region), and the consumer may be able to detect this (Sih 1987). As food rewards (Gilliam & Fraser 1987) or need for food (Milinski 1986) increase, consumers may venture into more dangerous areas. Any of these changes could modify spatial refuges for algae.

Small animals in streams are less vulnerable to predators in shallow water (Kneib 1987, Schlosser 1988, Power 1987). Small invertebrate and amphibian grazers exploit shallow algae in certain streams. In the Baron Fork of the Illinois River, for example, dense aggregations of snails forage on algal mats along pool margins, while grazing minnows feed on algae in deeper portions of the main channel (Matthews et al. 1986, Power et al. 1988). In the Rio Frijoles, tadpoles (*Bufo typhonius*) aggregate in water <10 cm deep for several weeks during the dry season (Power, personal observation). In general, however, small grazers in the Rio Frijoles do not attain densities sufficient to deplete shallow algae. Their numbers may be limited by high densities of small, predatory fishes such as the lebiasinid, *Piabucina panamensis*, and the characins *Astyanax ruberrimus*, *Hyphessobrycon panamensis*, *Gephyrocharax atricaudata*, and *Bryconamericus emperador*. These fishes are fast swimming, and for this reason may experience less hazard from birds during rapid forays into shallow water than would the relatively slow-moving grazing catfish. In addition, the capture of invertebrates can often be accomplished in seconds, in contrast to the persistent grazing required to detach small, often tightly adherent algae.

Spatial refuges from herbivory for algae did not change over the range of grazer hunger levels studied here or from 1978–80. Armored catfish that were experimentally starved showed no tendency to forage in shallower water after their release,

despite showing other behaviors that indicated that they were hungry. These results are consistent with observations of armored catfish over a 28 months period (Power 1984a). During this time, catfish did not occur in shallow water during the dry season, despite the abundance of their algal food there, and its scarcity in their deep habitat. Mortality rates (indexed by mark loss) showed no seasonal trends during this period, while somatic growth of pre-reproductive catfish ceased during the dry season (Power 1984a).

The disappearance of catfish from pens in 10 and 20 but not 30 and 50 cm of water is consistent with the hypothesis that risk from wading and diving birds increases sharply in water <20 cm deep. Despite the greater crypticity of *Rineloricaria,* more *Rineloricaria* than *Ancistrus* disappeared over the twelve days of this experiment. In retrospect, we noted that *Ancistrus* made good use of the minimal cover available in pens, wedging themselves behind support poles, while *Rineloricaria* remained on the gravel surface. The absence of predation on cages at the other two sites is likely due to the limited time (12 days) we had to carry out this experiment. Square pens were novel structures for Rio Frijoles herons and kingfishers, and it would not be surprising if some period of habituation would need to elapse before wild birds were ready to attempt foraging inside them.

The data from this study are inadequate to assess whether hunger increases emigration from pools by catfish. Hunger-related movement could account for the close tracking by catfish of food availability among stream pools (Power 1984b).

Results from our experiments support the hypothesis that in the Rio Frijoles, fishing birds constrain depth of grazing by armored catfish, producing a shallow refuge for attached algae. We predict that such patterns will be clear and recurrent in communities in which herbivores (1) are large and voracious relative to the size and growth rates of their foods, (2) avoid predation risk over a wide range of hunger levels, and (3) can endure prolonged food deprivation. Lotic fishes that graze attached algae exhibit these characteristics. As a result, grazing fishes and their predators produce and maintain striking patterns in the communities

of temperate and tropical streams.

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