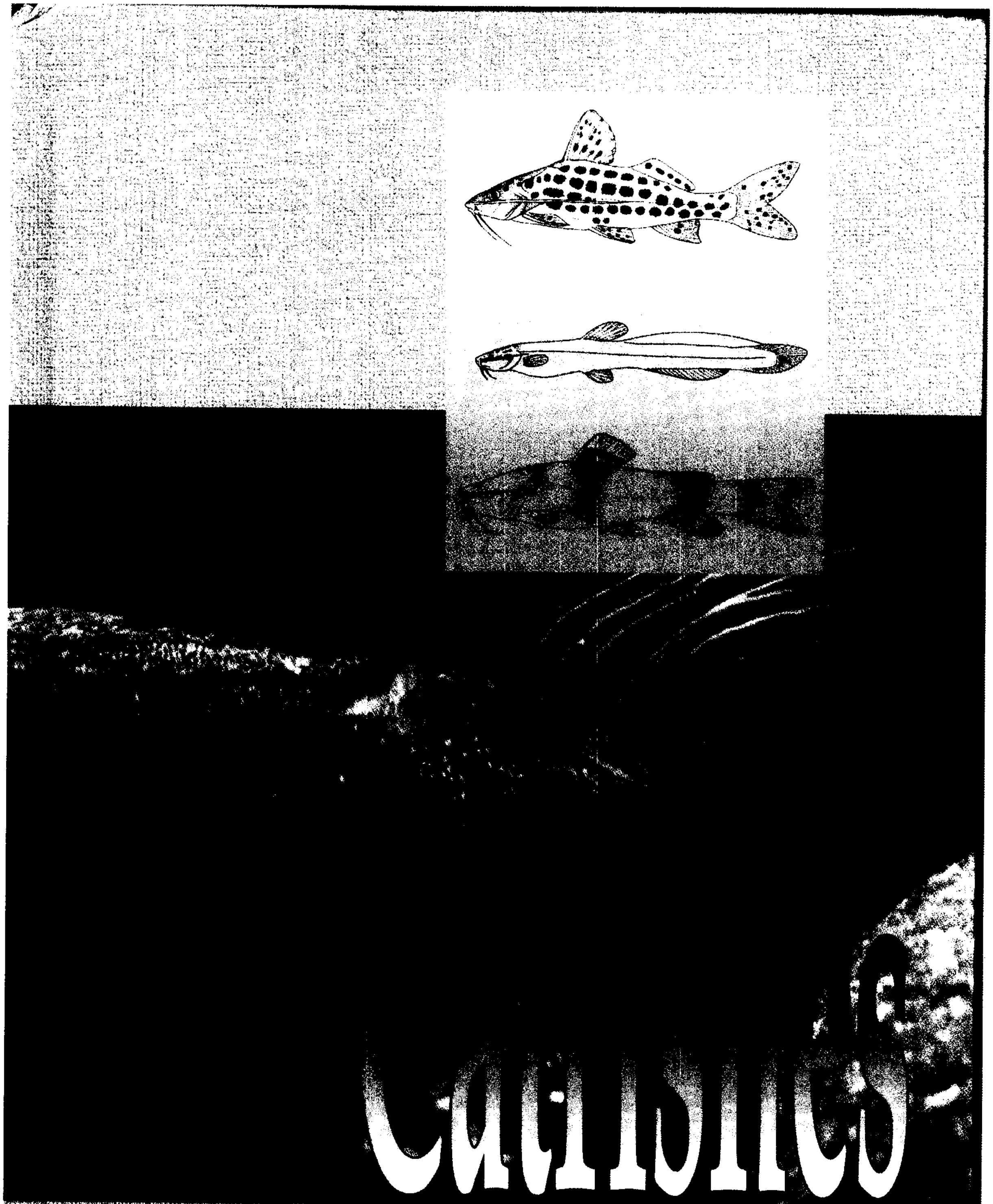

Catfishes

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CHAPTER

19

Life Cycles, Limiting Factors, and Behavioral Ecology of Four Loricariid Catfishes in a Panamanian Stream

Mary E. Power*

The Loricariidae, a Neotropical family of armored catfish, is the fifth most diverse fish family in the world (Nelson, 1994), with more than 600 species (possibly more than 800 species; Scott Schaefer, pers. comm.). Loricariids occur in small streams to large rivers from southern South America north to Panama (Burgess, 1989; Buck and Sazima, 1995). Loricariid populations have also naturalized in a few warm-water Habitats in North America where they have been introduced by humans (e.g., Barron 1964; Nico and Martin 2001). Ichthyologists and aquarists have long been fascinated by this group but relatively few long-term studies have documented their lives in nature.

In this chapter, I summarize field observations on the behavior and natural history of loricariids near the northern boundary of the family's

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natural distribution in the Rio Frijoles (9°9' N, 79°44'W). This stream drains secondary tropical rain forest of the Parque National Soberania in central Panama. The Rio Frijoles was once a tributary of the Chagres River but after construction of the Panama Canal, now empties into Lake Gatun. Four loricariids occur in streams of the Parque National Soberania: *Ancistrus spinosus* (Eigenmann et Eigenmann), *Hypostomus (Plecostomus) plecostomus* (Linnaeus), *Rineloricaria (Loricaria) uracanatha* Kner et Steindachner, and *Chaetostomus fischeri* Steindachner. Most of my observations are on *Ancistrus spinosus*, the most common loricariid in deeper stream pools of the Rio Frijoles. Here, I review field observations from a 28-month field study, describing loricariid responses to variation in their algal food, threats from various types of predators, physical stress from deposited fine sediments, and seasonal expansion and contraction of their habitat. The factors that limit these catfish vary as fish grow from eggs to juveniles to subadults and reproductive adults, and also seasonally, with hydrologic contractions and expansions of their habitat. Their responses to heterogeneity and change in their environments are constrained by their adaptations and may well influence their fates as Neotropical streams change under increasing impact from human land use.

MORPHOLOGICAL EQUIPMENT

Loricariids are not only speciose, but remarkable for their aspect diversity (sensu Rand, 1967). Body forms range from stout and compact to thin and elongate. Certain species have striking color patterns and appendages including bizarre, often sexually dimorphic spines, tentacles, and fin filaments, whose functions are largely unknown. Nonetheless, loricariids share characters that bespeak their benthic habits. Dermal bony plates armor most of the body except for the ventral belly. Swim bladders are reduced or absent. Their entirely ventral suctorial mouths have four comblike tooth plates with which they scrape food from surfaces. They also cling with their mouths, resting upside down under ledges or logs, or locomoting up waterfalls (Gradwell, 1971; Grzimek, 1984). Opercles of loricariids are small and entirely ventral (Fig. 19.1), protecting the Gills from nipping characins or poeciliids, but possibly exposing them to fouling or abrasion on sandy or silty surfaces. Several species of loricariids can use their digestive tracts as accessory air-breathing organs under hypoxia

Fig. 19.1 Small ventral opercle slit of a male *Ancistrus spinosus*.

(Gradwell, 1971; Gee, 1976; Kramer and Graham 1976), or in acidic or H_2S-rich waters (Brauner et al., 1995; Armbruster, 1998).

REPRODUCTION

Many loricariids exhibit male parental care of eggs and early fry. While males of some species carry eggs under large flaps of their lower lip, most loricariid fathers guard eggs and hatchlings in protected nest cavities.

Young *Rineloricaria uracantha* and *Ancistrus spinosus* begin their lives as eggs in their father's nests (Fig. 19.2; Power, 1981; Moodie and Power, 1982). Suitable nest sites appear to be in short supply for both species and may limit recruitment in the Rio Frijoles. Most of the *Ancistrus* nests I observed were in hollow logs, although I found one male *Ancistrus*, smaller than other breeding males, tending eggs in a narrow hole in a limestone bedrock. He occupied this cavity when it was only 10 cm beneath the water surface and abandoned it as the water level fell during the dry

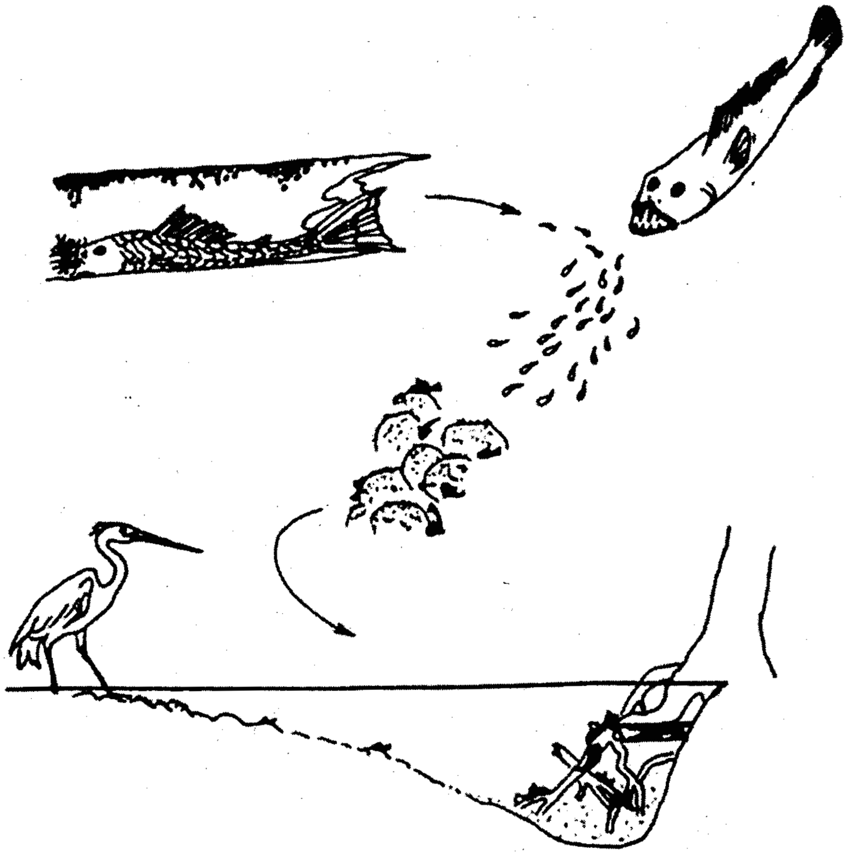

Fig. 19.2 Life cycle of *Ancistrus spinosus*. Top: The brooding male is larger than drawn here and usually braced by his pectoral spines so as to block access to the nest. Middle: Young of the year that escape from pool predators after fledgings move into nursery riffles. Bottom: When they attain Standard Lengths of about 4-5 cm, young fish move back into deeper pool Habitats.

season. The hollow logs in which *Ancistrus* nest must have openings close in diameter to the width of the anterior body of the breeding male. The father served as a kind of "armored cork", plugging the entrance against potential predators of his young, such as characin fishes (e.g., the active and ubiquitous *Astyanax ruberrimus*) and freshwater crabs (*Potamocarcinus richmondi*). Crabs are found in hollow nest logs when these are not occupied by breeding male *Ancistrus*. The size at which their exposed dorsal armor is hard enough to resist puncture by large crabs may set the

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lower size for breeding for male *Ancistrus* in this stream. I have seen these crabs eating loricariids alive (a 10 cm SL *Rineloricaria* and a 6 cm SL *Hypostomus*), which had backed up into their claws under rock ledges.

Ancistrus, normally sedentary within their home pools, will travel fairly long distances to find a suitable log. One marked male, first captured in early May (late dry season) in a pool in the upstream end of a mapped 3 km study reach, was resighted the following August in a pool 800 m downstream. He was lodged in a hollow log caught in a debris jam lodged in an undercut beneath the roots of a riparian fig, *Ficus insipidus*. The male was always in this nest when I checked it almost daily and on four nights over the next two months. Several females laid yellow eggs (different shades of color suggested different mothers), ca. 2 mm in diameter, attached in dense monolayers to the walls of the log. This *Ancistrus* reared two broods of fry in the same log. In early October (late rainy season), he was seen for the first time since August outside the nest, which was briefly occupied by a crab. Several days later, however, he was again fanning in the nest, which had received its second batches of yellow eggs. The father tended these eggs through October. In November, the nest log was blown away in a flood, and by early December (early dry season), this individual had traveled 800 m back upstream, crossing ten pools and ten shallow riffles to occupy the same recess under a rock ledge where he had originally been captured.

Male *Ancistrus* attain a larger size than females and appear to be larger at first reproduction (ca. 12-15 cm SL vs ca. 7-9 cm SL for females). When *Ancistrus* are 6-7 cm long, males begin to develop a soft spongy area on their snouts, from which a forest of snout tentacles (called rostral cutaneous processes by Ono (1980)) eventually proliferates. On older or larger males, these tentacles grow longer, denser, and more multiply forked. Both the tentacles and the spongy area hypertrophy and shrink periodically on large male *Ancistrus* in the wild, probably reflecting hormonally driven breeding cycles. Male brooding behavior suggests a Function for these tentacles. Guarding males insert their heads into the nest log, brace against its walls with stout, locked pectoral spines, and arch their unarmored bellies forward into the log, their dorsal armor facing outside. They fan water towards their ventral mouths with their large pelvic fins. The father's anterior body may block flow of fresh water into stagnant recesses of the log where the eggs and young fry are developing. Carter and Beadle (1931) observed *Ancistrus anisiti* brooding eggs in holes of the banks of swamps in the Paraguayan Chaco and noted that the oxygen requirement of these eggs was lower than for eggs of ictalurid catfish. For hatched fry, however, hypoxia may be more of a problem. When the breeding marked male described above was pulled from his nest log, many of the 427 18-mm SL fry I counted in his nest were clinging by their mouths to his snout tentacles. Tentacles may deliver oxygen to the young, a "male placental" Function once hypothesized for the anal fin of brooding male lungfish. This hypothesis would be supported if the rostral surfaces of males are well vascularized, especially if vascularization hypertrophies just prior to brooding. Ono's (1980) ultrastructural morphological study revealed microridges on *Ancistrus* snout tentacles (and also on the anteroventral oral disk and body surface). One Function proposed for these microridges in fish skin is to increase surface area for gaseous exchange (Hawkes, 1974). *Ancistrus* snout tentacles have also been hypothesized to have a gustatory Function (Ono, 1980), like barbels of other catfish. This sensory hypothesis is not exclusive with the male placental hypothesis proposed here. Sensory requirements seem unlikely to explain the expansion of soft rostral epidermis and engorgement of snout tentacles during brooding, however, because males do not feed while brooding. During the months it occupied its nest, the marked male lost weight (Power, 1981: table 4-1). Nesting males also probably do not need to seek females.

Male reproduction appears more limited by nest logs than by females. Females in turn may find males with adequate nest logs the factor most limiting their chances of successful reproduction. Nest logs were sufficiently limiting for *Ancistrus* that individuals pulled from their nests (so that I could inspect eggs or fry) immediately re-occupied them. Young males, within days, occupied artificial nests that I created by lining large glass jars with bark and half burying these in the gravel beds of pools. In the short (several-week) trials I conducted, however, no eggs were lain in these occupied artificial nests.

G.E.E. Moodie was more successful in a longer study of reproduction by *Rineloricaria (Loricaria) uracantha* in artificial nests. Like *Ancistrus*, *Rineloricaria* appears limited by appropriate nest cavities. This smaller, slender species lacks snout tentacles and must locate hollow submerged stems with flow-through water (Moodie and Power, 1982), such as hollow *Cecropia* stems just large enough to accommodate breeding males 2 cm at their widest point across the pectoral girdle. Male *Rineloricaria* readily occupied and reproduced in 2.54 cm diameter PVC pipes that Moodie deployed in the Rio Frijoles. Mature male *Rineloricaria* have wider, rounder snouts than females and, unlike females, develop jaw bristles along their lateral edges. Moodie also noted a second dimorphism: males could swing their pectoral spines forward to lie nearly parallel with their jaws, while females could only swing their pectoral spines far enough forward to project out from the body at a 90° angle (Moodie and Power, 1982: fig. 1). This posture potentially created a grasping organ for the males (by pinching objects between the jaw bristles and the pectoral spine), which Moodie thought might be used to manipulate females in the nest. It is possible (although not an interpretation favored by Moodie) that males might use their grasping ability to prevent superfluous females from entering nests and injuring or dislodging older eggs, once nests were filled. Multiple females laid eggs in his artificial nests and like *Ancistrus*, *Rineloricaria* males would stay with the nests even after they had been withdrawn from the water, opened to inspect eggs, closed and returned to the stream. Like *Ancistrus*, *Rineloricaria* males that have obtained a nest will brood several successive clutches of eggs (up to five for *Rineloricaria* (Moodie and Power 1982)).

I never observed nests of *Hypostomus* or *Chaetostoma* in the Rio Frijoles. These species may have nested deep under rock ledges or in holes that appeared in clay banks. *Hypostomus plecostomus* occupied burrows dug in firm clay banks. I observed a large individual rubbing the rough leading edge of its pectoral spine against a clay bank near a group of other holes. This motion looked like digging behavior. The holes could have been made by prawns (*Macrobrachium* sp.) that occurred in the stream, however, or by tree roots projecting into the flow that had rotted away. Neither *Chaetostoma* nor *Hypostomus* showed any apparent sexual dimorphism. *Hypostomus* (Lowe-McConnell 1967) and possibly *Chaetostoma* rear their young in bank holes.

ONTOGENETIC HABITAT SHIFTS (FIG. 19.2)

When young loricariids are 18 mm long SL (*Ancistrus*) or 12 mm SL (*Rineloricaria*), they leave the father's nest. While I have never witnessed a fledging episode, these must be times of great mortality, as soft, weakly swimming young catfish are readily eaten by common fishes in the stream (*Astyanax*, *Bryconamericanus*, *Piabucina*). Young loricariids must exit from a pool that is full of swimming predators, many of which are active 24 hours a day. Those that survive move into shallow riffles, where they can take cover in interstices among cobbles. I rarely observed armored catfish less than 3 cm SL in pools, or in water > 30 cm deep. On the few occasions when I witnessed a young of the year (yoy) *Ancistrus* (ca. 2 cm SL) traversing pools, it would edge across the stream margin near the surface, harassed by characins that struck at it in rapid forays from deeper water. Young loricariids reared in shallow riffles where they grazed algae. (Juvenile *Rineloricaria* include insect larvae in their diets and become more exclusively algivorous with size or age (Pineda, 1975). Young riffle-dwelling loricariids did not appear to be food limited, as algal standing crops in riffles were higher than in pools (Power, 1984a). Primary productivity was also probably elevated by the greater flux of dissolved nutrients in flowing water (Whitford and Schumacher, 1964) and increased insolation relative to beds in deeper pools. Although their armor was not yet hardened, predation pressure on young loricariids was probably reduced by their habitat selection. The Gape-limited aquatic predators to which they were most vulnerable avoided water shallower than 20 cm, where these characins, gobies, and other larger fishes were themselves at risk from diving and wading birds that frequented the river (Power 1984a, 1987). Loricariids smaller than 3-4 cm could hide under cobbles from these birds. When they outgrew this cover, at 4-5 cm SL, they also began to outgrow their vulnerability to most of the Gape-limited swimming predators in pools, and juveniles at this size (probably within their first year of life) moved into deeper pools.

In pools, subadult loricariids entered a crowded environment in which they became limited by food for most of the year. Standing crops of algae in pools were so scant that on substrates > 20 cm deep, algae were not macroscopically detectable (substrates did not even feel slippery). Microscopic sampling revealed only scant cover of very small, adnate diatoms (primarily *Achnanthes* sp. (Power, 1984b)). Visible accumulations of algae occurred, however, along pool margins on substrates < 20 cm deep, which grazing catfish appear to avoid due to their vulnerability in shallow water to wading and diving birds (Power, 1984a, 1987; Power et al., 1989). These birds fish most commonly and effectively in water < 20 cm deep, possibly because fish there have too little time to escape between the surface splash and the strike (Kramer, 1983; Power, 1984a). Along the Rio Frijoles, these shallow substrates were largely avoided even at night (Fig. 19.3), although there was some tendency for loricariids, particularly the smaller size classes and more cryptic species (*Rineloricaria*) to shift to

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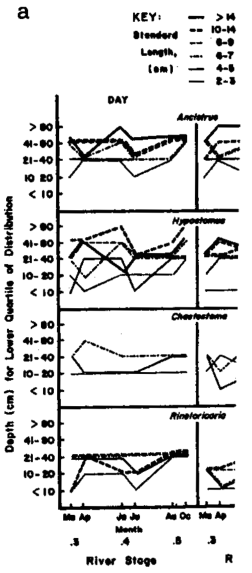

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slightly shallower Habitats in darkness (Power, 1984a). Night-fishing tiger Herons occurred along the Rio Frijoles. In other Habitats, these Herons have been found with "fair-sized, bony fish" in their stomachs (Wetmore, 1965). The avoidance of shallow water by grazing catfish allow "bathtub rings" of algae to accrue along shallow pool margins, which persist even in the dry season, when larger catfish in pools are most food limited.

SEASONAL CHANGES

Pool-dwelling loricariid catfish showed zero or negative Growth in the dry season (Power, 1984a). These weight measurements may have

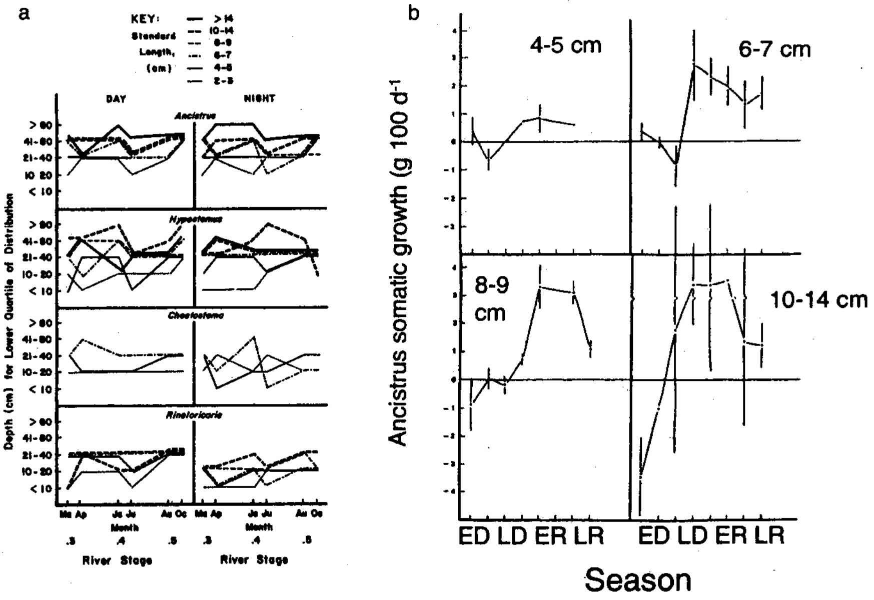

Fig. 19.3 **a.** Depth quartiles (shallowest depth such that at least 25% of the individuals of a given species and size class occur at that depth or less) for four species and six size classes of armored catfish. Quartiles estimated from data taken over two years during six snorkeling censuses of 180 m^2 quadrats distributed over a 3 km reach. Twice during the rainy season (August, October), the dry season (March and April), and during transitional months (January and June), physical conditions within each quadrat were measured, and then loricariid numbers in quadrats were counted on two days and two nights during the following week. **b.** Growth rates of *Ancistrus* of different length intervals, with two standard errors. ED = early dry season (December through February); LD = late dry season (March and April); ER = early rainy season (May and June) and LR = Late rainy season (July through November). Records are from marked, recaptured, and reweighed individuals; only records that fell within the seasonal intervals delimited were used. (After Power, 1981).

underestimated nutritional deprivation during the dry season, as a subsequent study (Power, 1984c) suggested that starving *Ancistrus* could substitute water for fat in tissues. With the onset of the rainy season, as stream flow deepened, the catfish were able to move into areas formerly too shallow to graze and showed a Growth pulse (Fig. 19.3b). Growth slowed after they had depleted the higher standing crops of algae formerly refuged in shallow water but remained positive throughout the rainy season. Seasonal changes in base flow discharge in the Rio Frijoles were modest and the channel habitat did not obviously expand, because much of the channel was fairly trapezoidal in cross section. What did expand by a factor of three, however, was the amount of substrate under > 20 cm of water. The expansion of this "safe" habitat was tracked by a corresponding 3-fold decrease in the density of loricariids. During my first field season, I was surprised after the transition from the dry to the rainy season to find loricariids suddenly sparser. I searched the entire river for migrating groups of loricariids and investigated episodic predation (by migrating cormorants or aquarium collectors) as a possible cause for drop in loricariid density, mistaking it for a drop in abundance. It was only after constructing bathymetric maps of the 3-km study reach, drawn from detailed surveys that enabled resolution of 10-cm depth contours in the channel habitat, and learning of the depth tolerances of loricariids, that I appreciated that seasonal expansion of this critical habitat stratum was the cause of the density changes. This interpretation was confirmed during the next year's transition from the dry to the rainy season, when the first flood elevated stream stage. After this flood, the water table in the surrounding watershed remained low, so stream discharge subsided within days. Censuses of quadrats marked on the bed showed that catfish spread out with the high flow, becoming 3-fold less dense, then reconcentrate with the abating flow, regaining their preflood density within a week, i.e., within such a short period that migration or recruitment could not have accounted for the observed density fluctuation (Power, 1981).

SENESCENCE

Another indication that their conservative space use protects larger *Ancistrus* from predation is that a few older individuals (large males) grew increasingly easy to capture over time, as if they were becoming diseased or senescent. Some of these individuals showed aberrations of the eyes—the iris which normally projects down to make a horseshoe-shaped pupil

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Fig. 19.4 Senescent *Ancistrus* with eroded iris and cloudy pupil.

was eroded and hence these older individuals had ragged, circular pupils that also appeared cloudy (Fig. 19.4). Despite their blindness or other infirmities, these older individuals persisted many months in their natural environments, suggesting that they remained safe from predators if they avoided shallow waters where mammals and birds fished.

HABITAT PARTITIONING

Loricariids are the only major grazers of algae in deeper pools of the Rio Frijoles; macroinvertebrate scrapers were sparse and virtually absent in deeper Habitats. Frog tadpoles occurred seasonally but only along shallow stream margins (depths generally < 15 cm). Some poeciliids, cichlids, and characoids browsed algal filaments but did not scrape surfaces. Given that larger loricariids were food limited for much of the year (as evidenced by the fact that they grew at less than their potential maximum rates), one could infer that they compete with each other for limited food or grazing substrate. According to classical niche theory, one might expect that species would partition grazing substrate to reduce interspecific competition.

There were some differences among the species in tendency to use particular substrates. *Ancistrus* was common on large submerged logs, which they grazed and used for cover (nimbly circling around logs to keep out of my reach, for example). They also grazed bedrock, large boulders, cobbles, and consolidated clay banks. These substrates were also commonly used by *Hypostomus*, which were particularly abundant on the clay banks. *Rineloricaria*, with its narrower mouth and more cryptic body, was abundant on clay and bedrock and also on cobbles and pebbles in the shallower pool heads and tails, and in shallower mid-pool environments. *Chaetostoma fischeri*, the one species in the Rio Frijoles that could not use its stomach as an accessory air-breathing organ, was restricted to constricted reaches where the flow was both fast and deep. There was some rough color matching among the species with the substrates—*Chaetostoma* was dark brown with gold glints and often matched the dark rocks in the rapids where they occurred, while *Hypostomus* and *Rineloricaria* were both dun colored, matched to clay and mudstone substrates. Black *Ancistrus* was the color of submerged logs that retained their dark bark. I was not overly impressed with substrate specialization or partitioning among the species, however. In the dry season, as food became more limited, species overlapped more in the types of substrate they used (Power, 1981, 1983), as documented by Lowe-McConnell (1975) for Neotropical fish stranded in isolated pool "lifeboats" in northern South America. These observations contradict theoretical predictions of increased niche separation to reduce competition during periods of resource limitation (Zaret and Rand, 1971).

RESPONSES TO FOOD QUALITY AND RENEWAL

Armored catfish generally live within bounded pool Habitats and eventually regraze sites on pool substrates. If an individual returns to a previously grazed site too early, scant algae will have regrown. Buck and Sazima (1995) observed that sites cleared by loricariids in the Ribeirao da Serra, a small, clearwater forest stream in southeastern Brazil, presented new algal Growth in about 24 h. Average return times of armored catfish in sunny pools of the Rio Frijoles, where the loricariids were most dense, were about 9-10 h (Power, 1984b), much shorter than the potential doubling time of diatoms even in productive environments. These short return times, along with the scant algal standing crops observed, suggested that Rio Frijoles substrates were heavily overgrazed. Undergrazing might also be disadvantageous for loricariid catfish, however. If loricariids returned after long time intervals, substrates would become silted. The deposited sediment could be either a stress or a food for grazers, depending in part on its organic content.

Seasonality influences the quality and persistence of sediments that are deposited on the substrates grazed by armored catfish. In the rainy season, these sediments are derived from clay-rich soils that wash into the stream during floods. Suspended sediments are deposited, or flushed downstream, depending on the concentration of suspended load in the water column on the recession limb of the flood hydrograph (Power, 1981). With several floods a month, the probability is high that large floods would scour away deposited sediments. Also, sediment accrual is reduced during the rainy season because even at base flow, currents over the bed are faster and boundary layers thinner. During the dry season low-flow period, sediment sifts down more continuously as organic matter in the water column settles onto substrates in still pools. This silt is displaced by *Ancistrus* and *Hypostomus* with head-shaking behavior with which they sometimes initiate grazing on heavily silted patches. It is also ingested and passed as consolidated feces. A feeding experiment in Panama suggested that the sediment was not a food for prereproductive (6 cm) *Ancistrus* and, in fact, imposed energetic costs estimated at up to 20% of their daily energy budgets (Power, 1984c). This cost may have been due to the costs of clearing sediment from their small, entirely ventral Gills (Fig. 19.1) by unknown mechanisms, possibly mucus sloughing or coughing. In Venezuela, however, Alex Flecker and colleagues have observed that another species, *Ancistrus triradiatus*, could grow on silt (A. Flecker, pers. comm.). Whether this disparity is due to difference in sediment quality or different adaptations of the Panamanian versus Venezuelan *Ancistrus* is not presently known, but merits further investigation, given the importance of identifying potential energy sources for these ecologically significant fish.

Siltation is a stress for Panamanian and apparently also for four species of Brazilian loricariids, which Buck and Sazima (1995) observed to initiate similar wiggling head-down movements when they commenced grazing on heavily silted substrates, movements which wafted sediment away from the area to be grazed. In both Habitats, previously cleared spots were regrazed by the same individual or other catfish (Fig. 19.5; Power, 1984c; Buck and Sazima, 1995). I often observed smaller loricariids

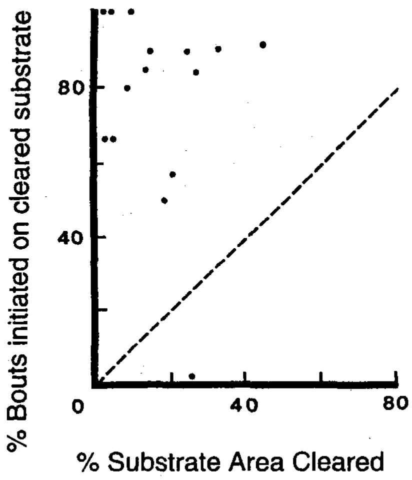

Fig. 19.5 Selectivity of *Ancistrus* for cleared substrate in enclosures. Points are the % of grazing bouts initiated on a given day on cleared substrate, plotted against the % of the substrate in an enclosure cleared on that day. If grazing bouts were initiated at random with respect to sediment, equal numbers of points should fall above and below the line X=Y (adapted from Power, 1981 and 1990).

regrazing sites opened in silted areas by larger loricariids. To test whether small fish would select such sites, I built a choice cage out of coarse plastic screen (6-mm mesh Vexar) with three chambers (Power, 1984c). The central chamber housed a small test *Ancistrus* (4-7 cm SL) and one of the side chambers housed a large individual (10-14 cm SL). Holes in the chamber partitions allowed the small but not the large catfish to move among chambers. When the cage was placed in heavily sedimented-areas, the small individual moved into the chamber with the large individual more frequently than would be expected by chance. When the choice cage was placed in sediment-free areas in the stream, there was no effect of the larger individual on the position of the small catfish (Power, 1984c).

In another experiment, catfish densities were reduced to ca. 0.1 their ambient densities in 4 m^2 enclosures built in a sunny pool that had previously supported up to 6 10-g individuals m^{-2}. Catfish regrazed small sites opened within enclosures significantly more than sites that had not been opened by grazing (Fig 19.5; Power, 1990). At these low densities, catfish grazing significantly reduced sediment standing crops and enhanced epilithic algal productivity and, surprisingly, algal abundance. Attached algal productivity and abundance were lower in the open habitat under the more intense ambient grazing regimen but still higher than in

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fish-free exclosures, in which thick carpets of silt accrued after several weeks (Power, 1990). This result suggested that loricariids could have "optimized" their harvests while grazing by foraging less frequently, and allowing more algal recovery between grazing bouts. That they in fact "overgrazed" in the open habitat suggested that they lacked a social mechanism, like territoriality, that could have increased the likelihood of "prudent grazing" by catfish.

AGNOSTIC INTERACTIONS

Given the intense intraspecific and interspecific competition for attached algae that Rio Frijoles loricariids experience for much of the year, one might expect to see interference as well as exploitative competition. I observed the four species grazing on gridded bedrock platforms in four stream pools by day and night (using dim underwater lights at night) and in the dry and rainy seasons over a two-year period. Most of the loricariids using these substrates were *Ancistrus*, with *Hypostomus* next in abundance. Interspecific interactions were relatively rare. In the few that I observed, *Hypostomus* and *Rineloricaria* rarely initiated interactions with *Ancistrus* and were almost always displaced by them. *Hypostomus* intraspecific interactions involved prolonged, gentle body contact and ended when fish drifted apart. The most common and intense interactions occurred between grazing *Ancistrus*. Out of a total of 647 5-minute *Ancistrus* grazing bouts observed, 111 bouts were interrupted by agnostic interactions (Power, 1984b). These occurred when two individuals of similar size grazing in close proximity bumped into each other and flared their opercular spines. In the most intense interactions that I observed, individuals pushed against each other with these spines. Such skirmishes were rare, brief, and immediately followed by flight of both participants out of sight to shelter under a rock ledge adjacent to their grazing platform. This behavior suggested that grazing catfish avoided more frequent or prolonged interference behavior because of the risk of attracting attention from aerial predators.

One observation of marked individuals suggested that *Ancistrus* knew each other as individuals. Two marked 6-7 cm SL *Ancistrus* hid after a skirmish. One returned and resumed grazing in the middle of a group of twelve conspecifics of similar size. Several minutes later the other *Ancistrus* returned and worked its way through this group, ignoring marked and unmarked individuals, to approach, then suddenly charge the first catfish and resume the skirmish. Olfactory individual recognition in ictalurids has been demonstrated experimentally (Todd et al. 1967).

The frequency of skirmishes did not influence *Ancistrus* Growth. Although interference episodes were 2-4 times more frequent in crowded groups of *Ancistrus* in sunny, productive pools than in sparse groups in dark pools, the average Growth rates of individuals in all of these pools was statistically indistinguishable. Similar somatic Growth rates, particularly of prereproductive individuals, suggested that the interference behavior imposed insignificant energetic costs (Power, 1984b; Oksanen et al., 1995) and did not impede individuals from closely tracking variation in algal Growth rates on the pool-to-pool scale over kilometers of stream reach.

IDEAL FREE DISTRIBUTION AND PRODUCTIVITY TRACKING

Because they are not apparently constrained by social dominance or pool-dwelling predators, all pool-dwelling loricariids could presumably enhance their fitness by closely tracking large-scale (pool-to-pool) variation in the availability of their algal food. In fact, loricariids tracked algal productivity quantitatively in pools distributed over a 3 km reach of the Rio Frijoles. Algal Growth rates varied 16-fold among these pools, because of variation in forest canopy shading stream substrates. I censused 16 pools distributed over the 3 km study reach of the river for 12 consecutive months by snorkeling through them and counting loricariids, including individuals hiding under ledges, which I detected with a small underwater flashlight. Catfish densities (both in terms of individuals and biomass) scaled to the area of grazeable (flat bedrock) substrate was linearly related to the relative productivity of a given pool. Measurements of algal Growth and depletion by collective loricariid grazing suggested that these rates were similarly balanced in the 6 dark, 6 half-shaded, 6 moderately sunny, and 3 very sunny pools. As Fretwell and Lucas (1970) predicted for animals able to achieve an Ideal Free Distribution, standing crops of algal food, somatic Growth rates of prereproductive*Ancistrus*, and survivorship of all *Ancistrus* were similar among the 16 sunny, half-shaded, and dark pools censused monthly for one year (Power, 1984b; Oksanen et al., 1995).

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PROSPECTS OF STREAM-DWELLING LORICARIIDS UNDER LAND-USE CHANGE

In the Neotropics, as in the rest of the world where humans have removed natural vegetation cover and built roads, stream Habitats are degraded by excessive loading of fine sediments. Impacted streams become shallower and wider and lose their deeper pools and undercut banks, eliminating breeding sites and adult habitat for loricariids. Coarse cobbles become embedded, eliminating interstitial cover for young-of-the-year loricariids and other fishes and invertebrates in riffles. Observations of degraded streams in agricultural or grazed lands of Brazil and Venezuela suggest that the most serious impact on loricariids may come from reduction in nesting and adult Habitats. Loricariid populations in such streams are dominated by young of the year, which probably do not survive their first year. Where loricariids lack structural cover and are also possibly subject to more human predation, their activity appears to become more exclusively nocturnal than in the Rio Frijoles.

In the Rio Las Marias in the Andean piedmont of Venezuela where loricariids and other fishes have been studied by Alex Flecker and his students and colleagues for 15 years, loricariids are largely nocturnal and numbers and biomass are dominated by young of the year. The Rio Las Marias also has other vertebrate algal grazers and detritivores in abundance, including ranid tadpoles, and a specialized characoid grazer, *Paradon apolinari,* in addition to five grazing loricariids (*Ancistrus triradiatus, Chaetostoma milesii, Hemiancistrus, Hypostomus,* and *Panaque)* (Flecker, 1992). Although fishing birds were more abundant and diverse around the Rio Las Marias than the Rio Frijoles, "bathtub rings" of algae did not occur. The predominant young-of-the-year loricariids and fast-swimming, unarmored algivorous characoids such as *Paradon* graze more in shallow water than the larger loricariids that dominate the Rio Frijoles.

Habitat conservation and restoration targeted at loricariids and other stream fishes with similar habitat requirements, would entail control and reduction of fine sediment loading, deepening stream pools, adding complex structures such as log jams, and replanting large riparian trees. The riparian Neotropical figs (*Ficus insipidus, Ficus* spp.) may be particularly effective in tropical stream restoration. Large figs develop long horizontal woody roots that grow back into cut banks of pools as streams migrate laterally under the trees. These snaky root systems continue to support the tree even as older roots become undercut. This growth adaptation produces cave-like undercuts that extend several meters under the bank, which are excellent Habitats and breeding sites for larger fish.

Like many fishes, loricariid populations may be potentially quite resilient. Adults are long lived (several decades) with moderate lifetime fecundity. Many species have adaptations to cope with stresses such as transient hypoxia and intermittent substrate sedimentation. Long-lived loricariids, can therefore, persist in unsuitable Habitats with many years of successive recruitment failure, via the "storage effect" (Warner and Chesson, 1985). As environmental stresses grow more prolonged or chronic, however, habitat loss will constrict the life history bottlenecks of loricariid catfish past the point of recovery. We are at risk of losing many loricariid species before we have even begun to appreciate their spectacular diversity and the highly evolved morphological, behavioral, and ecological adaptations that mold their lives in nature.

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