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Detritivory in neotropical fish communities

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Synopsis

Fish communities of major river systems in South America contain a high proportion of detritivorous fishes in the families Prochilodontidae and Curimatidae. These families include important fish stocks that in some regions comprise over 50 percent of the community ichthyomass. As a group, detritivores have anatomical-physiological adaptations for collection and digestion of detritus, but the actual mechanisms of these presumed adaptations have to-date only been inferred. Dietary requirements have not been identified. Behavioral adaptation is implied by feeding habitat selection but its nutritional significance is unknown. Because many of these species have commercial importance, and because ongoing construction of impoundments threatens to disrupt seasonal migrations between spawning and feeding areas, an understanding of the feeding biology of detritivores is important.

The number and distribution of neotropical detritivorous fish

A fundamental discovery of ecological research during the last 15 years is that a principal route of ecosystem energy flux and material cycling is through the detritus food chain. Although herbivores are conspicuous in their consumption of primary food resources, inconspicuous soil and sediment detritivores do much of the work in conversion of plant matter to animal biomass. The relative importance of detritivory varies from system to system, but estimates for some ecosystems attribute 90% or more of primary consumption to detritivores (Mann 1972).

Only a small percentage of fish species feed as detritivores (Lowe-McConnell 1975). Although many fishes ingest small quantities of detritus[1] incidentally while feeding on benthic prey, this has not been considered to be nutritionally significant. Other fishes may turn to detritus as a temporary diet when preferred foods are not available, but their rapid loss of condition during this period indicates they are ill-prepared to exploit a detritus diet (Lowe-McConnell 1975). The great majority of fishes feed as secondary or higher level consumers and rely on invertebrates as their link to the detritus base of the food chain (Eggers et al. 1978).

The exception to this rule is found in the tropics, where detritivorous fishes can dominate ecosystem ichthyomass. This is most evident in the neotropics,

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[1] The term detritus will be used to mean dead organic matter that has been altered in some way that renders it unlike its original living form, i.e. organic matter that has undergone some diagenesis. By this definition, I exclude from consideration allochthonous fruits and flowers that are important in the diets of fishes feeding in seasonally flooded forests.

especially in the great river systems of South America. Most of the abundant detritivorous fishes in these rivers are contained in two closely related families: Prochilodontidae and Curimatidae (Fig. 1). The Loricariidae are sometimes mentioned as possible detritivores, but recent data indicate they feed principally on algae (M.E. Power, this issue). Due to the vast dimensions and open nature of these riverine ecosystems, there are only a few quantitative estimates of the ichthyomass comprised by a single detritivorous species. For the Rio Paraná (Rio de la Plata system), Bonetto (1970) estimates from extensive survey data that *Prochilodus platensis* compromises 60% of the total ichthyomass. In the Rio Pilcomayo (Rio de la Plata system), *P. platensis* also makes up 'the major part of the fish biomass' (Bayley 1973). In the Rio Madeira (Amazon system), the nine species of Prochilondontidae and Curimatidae together appear to be similarly dominant (Goulding 1981). The distribution of neotropical detritivores extends far upstream, although they may diminish in importance in lower-order streams (Lowe-McConnell 1975, p. 208). They are abundant in floodplain pools (Bonnetto et al. 1969) and were once abundant in one of the few natural low-altitude lakes in South America (Lake Valencia, Venezuela) (Pearse 1920). In view of their abundance, these few detritivorous fishes must play major roles in ecosystem energy flux and material cycling and in the population dynamics of their respective fish communities.

In Africa, there are three groups of detritus feeding fishes: the Citharinidae, the Cyprinidae including *Labeo* sp., and some of the Cichlidae. Citharinids are closely related to neotropical detritivores (same suborder Characoidei, Nelson 1976), and they occupy identical habitats in low-gradient rivers, backwaters and floodplain pools. The cyprinid *Labeo* sp. occupies both riverine and lacustrine habitats in Africa, and the family Cyprinidae is entirely absent from the neotropics. Cichlids are widespread in both neotropical and African regions, but only in Africa do they appear as successful detritivores in shallow lakes and floodplain pools (Bowen 1979a). The detritivorous African cichlid *Sarotherodon mossambicus* has been introduced to freshwaters in much of the neotropical region, and in some areas large wild populations have become well established (Bowen 1980). Thus,

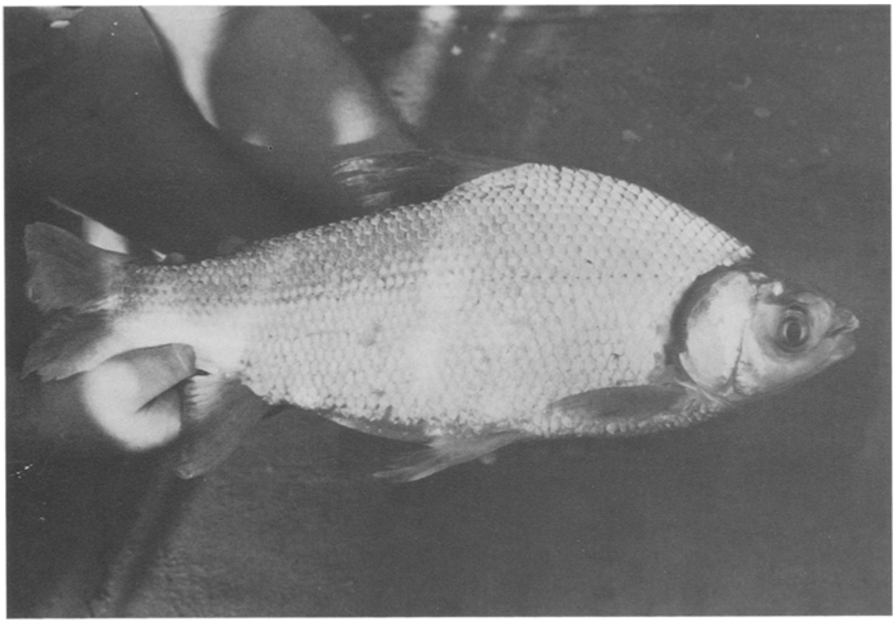

Fig. 1. Prochilodus platensis from the Riachuelo backwater, Rio Parana near Corrientes, Argentina.

it remains a mystery why neotropical cichlids have not evolved to take advantage of the detritus food resource.

For other regions, there is too little information to make useful comparisons. Detritus is clearly present in the diet of many temperate fishes, especially cyprinids, freshwater clupeids and catostomids. It will be essential to quantify the role of detritus in the nutrition of these groups before the trophic identification is certain.

Adaptations to detritivory

Studies of *S. mossambicus* indicate that two types of adaptations are important to the success of detritivorous fishes: morphological adaptations of the digestive system and behavioral adaptations for location of detritus (Bowen 1979a, 1979b, 1980, 1981). Observations reported for neotropical detritivores suggest similar adaptations.

The alimentary canal

The structure of the alimentary canal in *Prochilodus platensis* from the Rio de la Plata is described in detail by Angelescu & Gneri (1949). I found *Semaprochilodus* sp. and *Curimatus* sp. to have similar digestive tracts, although the relative dimensions of various structures may vary. Thus, general features of the digestive tract in *P. platensis* described by Angelescu & Gneri may be taken as representative of all Prochilodontidae and Curimatidae, although the function of this digestive tract has not been described.

In *P. platensis*, the protrusible jaws are weak and the lips bear fine delicate teeth. Observed in aquaria, the fish suck in fine, flocculant detritus from the surfaces of vascular plants and from the bottom. The teeth do not play a discernable role in this behavior.

Many detritivorous fishes confront difficulties associated with large quantities of inorganic matter, often mostly sand, mixed with organic detritus. When feeding from the bottom, both *S. mossambicus* and the ubiquitous estuarine and marine detritivore *Mugil cephalus* sort sediment in their oral cavity and reject inorganic matter while they retain organic detritus (Odum 1968, Bowen 1979a). The unusual oral cavity in *P. platensis* may improve the ability of the fishes to sort. Viewed in transverse section, the oral cavity has an inverted V shape (Fig. 2). In the anterior half, a single median dorsal, paired dorsolateral and paired lateral ridges extend into the dorsal portion of the cavity (Fig. 3a). The ridge margins are papillose, suggesting a sensory function. As sediment is sucked into the oral cavity, the coarse inorganic particles would be expected to settle into the lower arms of the inverted V, while flocculant organic matter would stay suspended. The five oral ridges could facilitate this

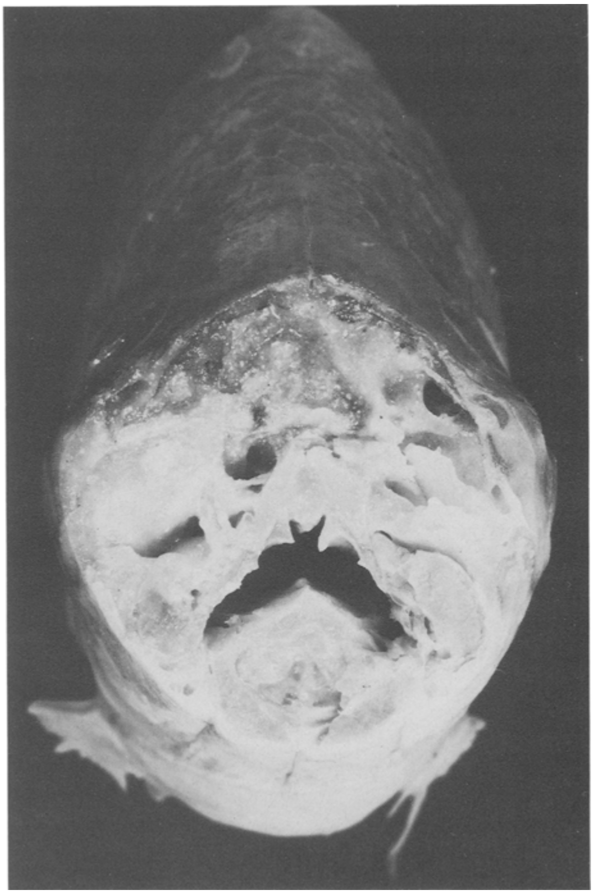

Fig. 2. Transverse section through the posterior oral cavity of *Prochilodus platensis*. Note the inverted V shape of the cavity and the ridges in the dorsal portion.

separation by reduction of turbulence, and the sensory structures assess the quality of the suspended organic matter.

Separation of flocculant detritus from water is probably achieved by the gillrakers. Unlike many fishes in which gillrakers form an essentially two-dimensional net, rakers on dorsal and ventral branches of the acutely bent gill arches intermesh to form a three-dimensional filtering structure. The individual rakers are fleshy, elongate structures oriented at an oblique angle to the gill arch. As suspended flocculant detritus is forced into this maze of constricted passageways, its adhesive nature, mucus on the rakers and the force of water flowing toward the aboral cavity would be expected to aggregate the detritus in a form that could be moved down the esophagus by peristalsis.

Epibranchial organs are present in the posterior pharynx (Fig. 3b). Similar structures are present in many lower teleosts, and their function appears to vary from species to species (Kapoor et al. 1975). Angelescu & Gneri (1949) suggested they produced mucus to aid passage of food through the esophagus, but stomach contents of freshly caught *P. platensis* I have examined do not include noticeably more mucus than those of *S. mossambicus*, which feed on a nearly identical diet but lack epibranchial organs. The food of *P. platensis* does enter the epibranchials, and thus their role in digestion merits closer scrutiny.

The stomach of *P. platensis* is divided into two parts (Fig. 4). The more anterior cardiac stomach is

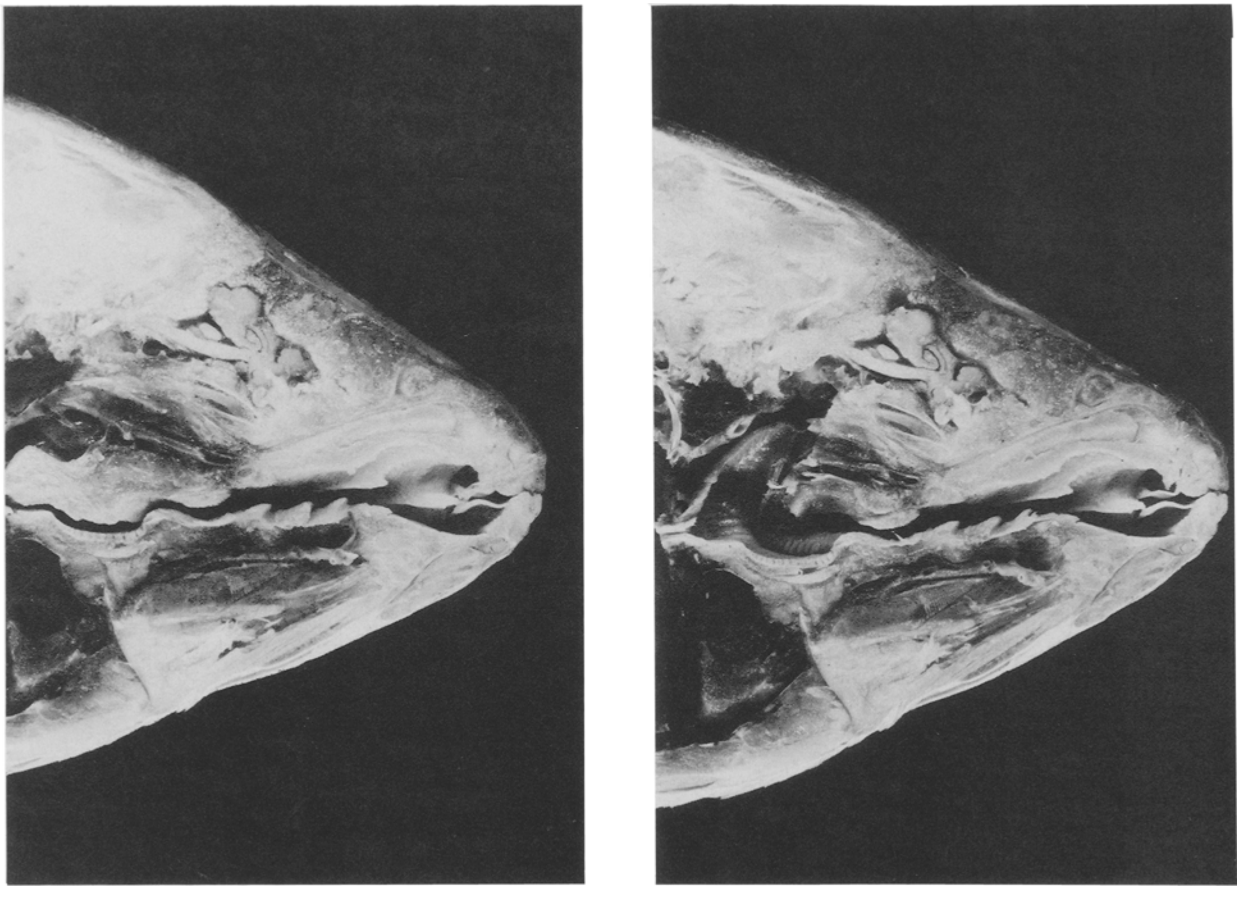

Fig. 3. Sagittal section of *Prochilodus platensis* head: in a – note the development and papillose margins of the oral ridges; in b – the dorsal pharyngeal pad has been removed to expose the left epibranchial organ.

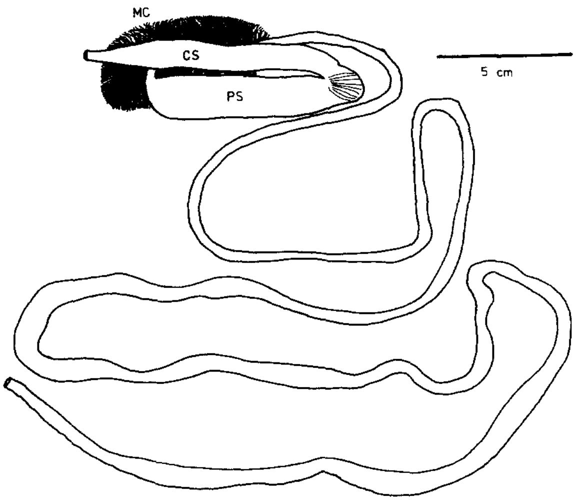

Fig. 4. Dissected digestive tract of a 31 cm (SL) *Prochilodus platensis*. (MC = mass of caeca, CS = cardiac stomach, PS = pyloric stomach.) In undissected specimens, anterior pyloric stomach is surrounded by the caecal mass. Traced from a photographic projection.

muscular but distensible so that it acts as a reservoir. The pyloric stomach is extremely muscular and nearly rigid, and serves to grind the food together with sand also ingested. This reduces the detritus to a small, nearly uniform particle size, conducive to enzyme-substrate interaction, and to peristalsis in the intestine (Fig. 5).

Similar grinding stomachs are described for *Citharinus* sp. and *Mugil* sp. (Kapoor et al. 1975), and Payne (1978) has suggested that gastric grinding in *Mugil* serves to disrupt algal cell walls. Since algae are rare in the diet of *P. platensis*, cell wall disruption is unlikely to be important for this species (Bowen personal observation). In sharp contrast to *Prochilodus*, *Citharinus* and *Mugil*, the stomachs in detritivorous cichlids are thin-walled, blind sacs. Many *Tilapia* and *Sarotherodon* sp. secrete gastric acid to unusually low pH values, frequently below pH 1.5. These conditions both disrupt cell walls (Moriarty 1973, Bowen 1976, Payne 1978) and fundamentally alter the chemical structure of detritus in ways that may facilitate intestinal digestion (Bowen 1981). Detritivores in the genus *Labeo* differ from others in that they lack a stomach and thus digestion in these fish appears to be a one-step, intestinal process.

Between the pyloric stomach and the intestine is a structure termed the pyloric chamber that gives rise laterally to short-branched second- and third-order chambers which finally branch into a mass of villiform pyloric caeca (Fig. 4). The caeca are approximately 1 mm in diameter and range from 3 to 10 mm in length. Angelescu & Gneri (1949) counted 3000 caeca in one specimen. Food from the

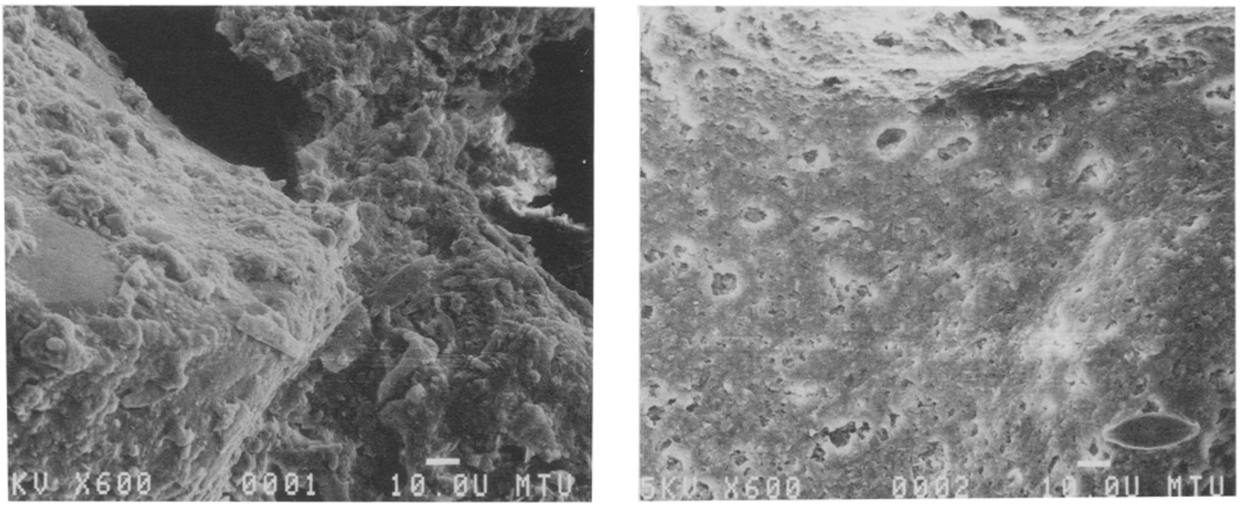

Fig. 5. Stomach contents of *Prochilodus platensis* from the Riachuelo backwater near Corrientes, Argentina: a – food from the cardiac stomach varies greatly in particle size; b – after grinding in the pyloric stomach, particle size is uniformly small.

pyloric stomach passes into the pyloric chamber, enters the caeca and is later extruded back into the pyloric chamber from which it passes on to the intestine. Food in the anterior intestine is often in the form of tiny strands with dimensions of the pyloric caecum lumen. From histological data, Domitrovic (personal communication) concluded the pyloric caeca are not secretory, but serve in post gastric assimilation. This differs from the largely secretory role ascribed to pyloric caeca in other fishes (Kapoor et al. 1975).

Although no sphincter separates the pyloric chamber from the intestine in *P. platensis*, the functional beginning of the intestine is found at the point immediately posterior to the pyloric chamber where the common bile duct delivers bile salts and intestinal digestive enzymes to the lumen of the gut. Two regions of the intestine are readily distinguished according to the type of folds formed by the intestinal mucosa. Folds in the upper third are circular and low in profile. In the lower two-thirds, partition-like, transverse folds that extend halfway across the lumen are found on alternate sides of the intestine space at 3 to 8 mm intervals.

Among fishes, the degree of intestinal development in length and mucosal folding is clearly correlated with trophic status, ranked according to relative intestinal development, carnivores < omnivores < herbivores < detritivores (Fryer & Iles 1972, Kapoor et al. 1975). This relationship is generally interpreted as a reflection of the resistance of different foods to intestinal enzymic digestion. Animal prey that have been masticated or processed in the stomach offer few barriers to intestinal enzymes. In contrast, plant and bacterial cell walls are very effective barriers. Even with well developed means for cell-wall disruption, intestinal digestion appears to be much slower in herbivores than in carnivores (Moriarty 1973, Bowen 1976, Caulton 1976).

A different sort of barrier may retard intestinal digestion of detritus. During the process of detritus formation, the chemical structure of the parent material is extensively modified. Many reactive sites previously available to digestive enzymes may be altered, or masked by other organic or inorganic compounds, such that few sites are available for enzymic hydrolysis. A study of intestinal digestion in *S. mossambicus* showed that the full length of the long intestine was necessary for maximum digestion of detrital amino acids (Bowen 1980). Had these amino acids been present in the form of protein (parent material), digestion would have been very rapid (Bowen 1981). It appears that detritivores confront special obstacles to intestinal enzymic digestion as a consequence of chemical changes that are integral to detritus formation, and a well developed intestine is needed to overcome these obstacles.

There are two ways in which the intestine may be developed. In *Labeo* and *Sarotherodon*, the intestine is exceptionally long: 15 to 21 and 8 to 10 times body length, respectively (Kapoor et al. 1975, Bowen 1982a, 1982b). In *Prochilodus*, *Curimatus* and *Citharinus* the intestine is relatively short (3 to 4 times body length), but the mucosal folds are extensively developed. Angelescu & Gneri (1949) estimate that mucosal folds increase the absorptive surface in the intestine of *P. platensis* by a factor of four. Thus, the available data indicate that the intestine is similarly well developed in each of these detritivores.

Although the above comparisons build an image of parallel adaptations developed to overcome common obstacles to digestion, truly definitive comparisons will require quantitative analysis of digestive processes.

Selective feeding

We can reasonably expect the flowing waters of neotropical rivers to provide a diverse menu of detrital food resources. Current velocity determines the size of detrital particles that settle out of suspension with fine particulate detritus accumulating only in the quiet backwaters. Watershed vegetation and water chemistry will determine the quality and quantity of dissolved organic matter that precipitates to form detritus in each tributary. As detritus is transported downstream, it is continuously modified by physical, chemical and biological agents that are likely to alter food quality.

Studies of *S. mossambicus* in Lake Sibaya, South

Africa, and Lake Valencia, Venezuela, have shown that selective feeding on high-quality detritus is the key to their success. In both lakes the amino acid content of diet varies across a wide range from low levels inadequate for simple body maintenance to high levels that support rapid growth (Bowen 1979, 1980). Those *S. mossambicus* that select high amino acid detritus grow rapidly and are in good condition. Apparently due to the conflicting demands of predator avoidance, adult *S. mossambicus* in Lake Sibaya feed on amino acid-poor detritus and suffer severe malnutrition as a result (Bowen 1979a). Similar work on *Citharinus citharinus* in backwaters of the Niger River has shown these fish select benthic detritus high in nitrogen (= amino acid?) (Bakare 1970).

Lowe-McConnell (1975) noted that, although organic detritus is abundant in all reaches, detritivorous fishes are generally abundant only in middle and lower reaches where fine-particulate detritus accumulates. Observations on the annual migratory cycles of several *Prochilodus* populations support her view. *Prochilodus* sp. ascend tributaries to spawn, usually during the rising flood cycle. Throughout the period of migration and spawning, they rely on large visceral fat reserves and do not feed (Lowe-McConnell 1975, Cannon personal communication). Once they have returned to downstream backwaters, feeding commences and the reserves are regenerated (Bayley 1973, Lowe-McConnell 1975, Cannon personal communication). Fishermen report that, within backwater areas, *Prochilodus* are commonly seen feeding in water less than 30 cm deep. A similar preference for detritus in shallow backwaters has been reported for mullet (Odum 1970). Is it possible that *P. platensis* select shallow backwater areas to feed because they contain detritus of superior food value?

Future research

In many parts of South America, detritivores are the principal species harvested in commercial fisheries (Mago 1972, Godoy cited in Lowe-McConnell 1975). In other areas, overharvest of predatory fishes may soon force the fishery to rely more heavily on detritivores (Goulding 1981). Increases in fishing pressure come at a time when these species face profound alterations of their natural environment by man. Several major impoundments are in various stages of planning and construction in the Orinoco and de la Plata basins. Some are planned without a fish-passage facility. For others the passage facility may not be properly designed. One species of *Semaprochilodus* is apparently unable to ascend rapids routinely negotiated by other fishes (Goulding 1981), and thus special design considerations may be required. Will species of Prochilodontidae and Curimatidae trapped below impoundments be able to spawn? Will those trapped above be able to find adequate feeding areas? What will be the effect of the increased lentic character of the system on the detritus food resource and the detritivore's ability to utilize it? These and other questions can only be answered by future research on detritivores.

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