Feeding and Digestive Functions of Fishes

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Preface

Understanding the biology of the innumerable number of aquatic species on our planet is the focus of sustained research efforts. Environmental degradation, management or rehabilitation of wild stocks, and the forecasted climatic changes are fueling interest in the study of the ecology, feeding behavior, and nutrition of aquatic animals in their natural habitat. In parallel, the rapid expansion of aquaculture in many parts of the world has supported vigorous research programs on nutrition and feeding of cultivated aquatic organisms. More than 250 aquatic species are cultivated on a commercial scale using a wide variety of production systems. This great diversity results in great opportunities and tremendous challenges. The number of scientific publications on nutrition and feeding of aquatic animals is ever increasing and our knowledge base is expanding rapidly.

The diversity of species and issues studied and the large number of papers published each year makes it very difficult to keep up with progress. It is highly desirable to occasionally review the state-of-the-art and progresses, identify gaps in our understanding, and pinpoint emerging issues. There are numerous books providing a good overview of state-of-the-art in fish nutrition. Numerous authors have reviewed in details the nutritional requirements of fish, notably from an aquaculture perspective. However, few books have specifically focused on feeding and digestion in fish in captivity or in their natural habitat. This book, therefore, attempts to fill what we think was a significant gap in the reference literature. Scientists actively involved in research on feeding and digestion in fish were invited by the editorial team on the basis of their expertise and track record. These investigators were given "carte blanche" as to the content and style of their contribution. The twelve chapters contributed by these investigators cover topics as diverse as feeding ecology of fish in their natural habitat, feeding behavior, digestive anatomy, biochemistry and physiology of different fish species at different life stages, the impact of diet on gastro-intestinal development and health, nutrition and disease resistance, and modeling conversion of food or feed inputs into biomass.

We believe this book contains a wealth of information and will be valuable to a wide variety of readers. However, it does not pretend to be exhaustive or perfect. It is mainly an attempt to allow sharing of knowledge, experience, and ideas. In the various chapters, a number of interesting and rather unique scientific analyses are presented and these may capture the interest of scientists and graduate students. Aquaculture specialists, fisheries biologists, students in natural and applied science programs, and fish feed manufacturers will find in this book relevant information suited to their diverse needs. We invite readers to approach the material in this book with an inquisitive mind. This book should initiate learning and rather complete it.

J.E.P. Cyrino, D.P. Bureau and B.G. Kapoor

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CHAPTER

1

Feeding Ecology of Fishes in the Brazilian Amazon - A Naturalistic Approach

Jansen Zuanon* and Efrem Ferreira#

INTRODUCTION

The Amazon system is composed by a multitude of rivers with varying water types and strikingly different productivities. This environmental diversity is accompanied by the presence of diverse fish species assemblages and ecological characteristics. Although a considerable amount of information about the trophic relations of the Amazonian fishes and their natural habitats have been generated in the previous few decades, most of the published literature deals only with descriptions of the main food items of the commercially most important species, and is based mainly on stomach contents analyses. We present here a quick look into the trophic interactions of the fishes and their natural environments, based on the diversity of the Amazonian fish fauna and its aquatic

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habitats. This chapter focuses on the main aquatic environments found in the Brazilian Amazon: the huge river-floodplain systems and their different water types; the multitude of small clear and black water streams that drains the "terra firme" (upland, non-floodable) forests, including their marginal temporary ponds; and the riffles and rapids zones of the rivers that drain the Brazilian and Guyana Shields and harbor a very rich and trophically specialized fish fauna.

White water river-floodplain systems sustain high primary productivity that is responsible for the major portion of the biomass produced in the aquatic environments in the Amazon. The flood pulse, a monomodal seasonal rising of the river level, is the most important factor influencing the life of fishes in the large rivers of the Amazon. The cyclic rising of the water level inundates a large area of riparian forest, and in the process makes available new habitats and an enormous variety of food items to the fish fauna. It is during this time of the year that the fishes can enter the flooded forests and feed on fruits and invertebrates that fall from the trees. The large black water rivers present an extremely low aquatic primary productivity but contain a surprisingly rich and diverse ichthyofauna. A low abundance of most species and a strong dependence on allochthonous food sources are the remarkable characteristics of the fish fauna of Amazonian black waters.

The Amazon forests are also drained by an endless number of small streams of clear or black waters which are characteristically oligotrophic and apparently sustain a low biomass of fishes. The nutrient-limited environment of the first-order streams is occupied almost exclusively by fishes that feed on allochthonous sources of food, such as terrestrial insects and other small invertebrates that fall from the trees. These fragile, low-productivity aquatic environments are being submitted to strong environmental disturbance, mainly derived from the deforestation of large areas for agriculture, pasture, and urban growth.

The clear water rivers that drain the Brazilian and Guiana Shields show highly variable chemical characteristics and primary productivity, and usually have a series of rapids and waterfalls along their courses. These turbulent zones are the habitat of many endemic fish species that rely on the local periphytic production as their main food source, which is exploited in a variety of specialized ways. The high periphytic productivity coupled with variations in mouth and teeth morphology and different feeding strategies allow for the presence of highly diverse fish fauna. The presence of many endemic species in the rapids also points out to the need for special conservation strategies since those areas are highly threatened by the construction of hydropower plants in the Brazilian Amazon.

The relationships between fishes and flooded forests probably represent the most remarkable biological interaction in the aquatic environments of the Amazon, and represent an important energy pathway between the terrestrial and aquatic systems. The knowledge of these intricate ecological interactions and the measurement of their impact on the regional economy may represent an effective way to preserve the magnificent flooded forests and the amazing diversity of aquatic environments in the Amazon.

The most remarkable ecological characteristic of the Amazonian ichthyofauna probably is its close relationship with the forest. The seminal work of Goulding (1980) in the Madeira River system depicted in detail the intimate relations of the fishes and the flooded forest, where fish acted as fruit and seed predators and simultaneously, as seed dispersers that help to maintain the high plant diversity of the riparian forests. Nevertheless, the Amazon system is composed of a multitude of rivers with varying types of water bodies and with strikingly different productivities. White water river-floodplain systems sustain high primary productivity, both by phytoplankton production in the floodplain lakes and the rapidly growing aquatic macrophytes that abound in the shallow marginal areas. These floodplains are responsible for the major portion of the biomass produced in the aquatic environments in the Amazon and also sustain intense commercial fisheries. The black waters of the Rio Negro and other Amazon tributaries represent the opposite situation, with an extremely low aquatic primary productivity but holding a surprisingly rich and diverse ichthyofauna (Goulding *et al.,* 1988). The clear water rivers that drain the Brazilian and Guiana Shield lie between these extremes, showing highly variable chemical characteristics and primary productivity (Sioli, 1984). Furthermore, these rivers present a series of rapids and waterfalls along the transition region between the Guianas and Central Brazilian plateaus and the main Amazon sedimentary basin. These riffle zones are the habitat of many endemic fish species that rely on the local periphytic production as their main food source, which is exploited in a variety of specialized ways.

This environmental diversity is accompanied by the presence of different fish species assemblages and ecological characteristics. Although the ecological interactions in the aquatic environments of the Amazon are still far from well known, a considerable amount of information about the trophic relations of the fishes and their natural habitats have been generated in the last few decades (e.g. Marlier, 1967, 1968; Knöppel, 1970; Soares, 1979; Goulding, 1980; Ferreira, 1981, 1993; Goulding and Carvalho, 1982, 1984; Santos, 1982; Carvalho and Goulding, 1985; Silva, 1993; Santos *et al.,* 1997; Sabino and Zuanon, 1998; Santos and Rosa, 1998; Zuanon, 1999; Walker, 2004). Most of the published data concerning the diet of Amazonian fishes deals only with descriptions of the primary food items of the commercially most important species, and were based mainly on stomach contents analyses. Furthermore, very few studies present information on the nutritional contribution of the various kinds of foods consumed by the fishes, which do not allow for a precise analysis of their relative importance on the fish diets. Although important, these approaches to the study of the feeding ecology of fishes usually do not allow for a comprehensive view of the diverse and complex interactions of the fish fauna in different biotopes. The available information in the literature usually presents generalized views of the trophic characteristics of the regional fish fauna, or comprises somewhat loose data regarding the diet of single species. In other instances, fish community studies end up with a multitude of data about a large number of species, so deeply transformed by multivariate statistical techniques that the beautiful trophic interactions that occur in the natural surroundings are not readily evident.

In view of these limitations, we aim to present a different look at the trophic interactions of the fishes and their natural environments, based on the diversity of the Amazonian fish fauna and its aquatic habitats. This chapter focuses on the main aquatic environments found in the Brazilian Amazon: the huge river-floodplain systems and their different water types; the multitude of small clear- and black-water streams that drain the 'terra firme' (upland, non-floodable) forests, including their marginal temporary ponds, and the riffles and rapids zones of the rivers that drain the Brazilian and Guyana Shields and harbor a very rich and trophically specialized fish fauna.

Most information presented herein is derived from the authors' personal experiences gathered during field activities and along several research projects developed in the Brazilian Amazon. We hope that this chapter will provide some new perspectives on the feeding ecology of freshwater tropical fishes, and stimulate a much-needed revival of the naturalistic approach to the study of the Amazon and its fishes.

RIVER-FLOODPLAIN SYSTEMS

The flood pulse, a monomodal seasonal rising of the river level, is the most important factor influencing the life of fishes in the large rivers of the Amazon (Junk *et al.,* 1989). The cyclic rising of the water level inundates a large area of the riparian forest, making available new habitats and an enormous variety of food items to the fish fauna. It is during this time of the year that fishes can enter the flooded forests and feed on fruits and invertebrates that fall from the trees. The extravasation of the water over the banks of the rivers also floods lateral depressions along the river channel, thus constituting more lentic habitats that function temporarily as true lakes, especially when the water recedes and these water bodies become isolated from the river channel (Plate 1.1).

In white water river basins, these lakes constitute the most productive natural aquatic environment of the Amazon (Junk, 1970, 1973; Sioli, 1984; Junk and Piedade, 1993), but the situation is markedly different in black water rivers. The low autochthonous productivity of black waters does not sustain a large biomass of fishes. A low abundance of most species and a strong dependence on allochthonous food sources are remarkable characteristics of the fish fauna of black waters such as the Negro River in the Brazilian Amazon (Goulding *et al.,* 1988). Even the reduction of adult body size (= miniaturization) has been hypothesized to represent an evolutionary strategy to minimize the energetic demand among Amazonian fishes (Weitzman and Vari, 1988). Clear water rivers are somewhat more productive and apparently sustain a larger biomass of fishes, mainly dependent of the periphyton production (e.g. Ferreira, 1993; Zuanon, 1999).

Floodplains have long been recognized as critically important habitats for the ichthyofauna, whereas the river channel itself has been supposed to serve mainly as migration routes for most Amazonian fishes (Junk *et al.,* 1989). Recent studies have revealed that the river channels harbor a rich fish fauna dominated by species of catfishes and electric knife fishes, but still poorly known with respect to trophic characteristics (e.g. Lundberg *et al.,* 1987; Cox-Fernandes *et al.,* 2004). In order to allow for a better understanding of such diverse and complex trophic characteristics and interrelationships, we choose to present information for each of the main habitat types recognized in these river-floodplain systems: the river channels, including the steep banks, beaches, and the channel itself (open water and bottom habitats); and the floodplain lakes, including the open

Plate 1.1

(Upper left) General view of a floodplain lake along the Amazon river margin. Note the floating meadows bordering the lake margins. Photo: E. Ferreira.

Plate 1.1 Contd.

water habitats, floating meadows and the flooded forests. Although present both at river and lake margins, the flooded forest is discussed among the floodplain habitats in function of its predominantly lentic characteristics.

River Channels

Probably one of the most obvious habitats along a river is its banks. The steep river margin usually constitutes a highly dynamic habitat that is composed of many different features, such as backwaters, eddies, small bays, and submerged woods. The calmer zones are commonly occupied by shoals of the pike characin *Boulengerella* spp. (Plate 1.1) and other opportunistic piscivorous species that ambush and pursue small characins moving along the river margins. The woody shores are the habitat of some large armored, sucker mouth catfishes like *Panaque* spp. and *Acanthicus hystrix* (Loricariidae). *Panaque* catfishes are known to feed on wood fragments scraped of submerged tree trunks and branches, although how the fish digests the cellulose is not well known (Nelson *et al.,* 1999). *Acanthicus hystrix,* the largest loricariid catfish (up to one meter long), is also frequently found foraging on the periphyton that grows in the submerged trunks. Large doradid catfishes like adult *Pterodoras granulosus* and *Megalodoras uranoscopus* congregate in the deep and calm bays to feed on insects, mollusks, small fishes and almost any edible organic particles. Shoals of the pimelodid catfish *Sorubim lima* are usually found in these habitats searching for small fishes, shrimps and worms close to the

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Plate 1.1 Contd.

(Upper right) A sandy beach in the Amazon River near Santarém, Pará State, Brazil. Photo: E. Ferreira.

(Second row, left) A small school of the pike characin *Boulengerella maculata* ambushing small prey fishes close to the banks of Araguaia River, Tocantins State, Brazil. Photo: J. Zuanon.

(Second row, right) The boldly patterned scale-eating characin *Exodon paradoxus* (Characidae) in field aquarium. Photo: E. Ferreira.

(Third row, left) A hematophagous candiru *(Vandellia cirrhosa,* Trichomycteridae) attacking a young tambaqui *(Colossoma macropomum,* Characidae) in aquarium. Photo: I. Sazima.

(Third row, right) A large Tambaqui *(Colossoma macropomum,* Characidae) taking a rubber tree fruit *(Hevea spruceana)* at the water surface. Photo: M. Goulding.

(Bottom left) A stingray *(Potamotrygon leopoldi,* Potamotrygonidae) partially buried in the sand in a beach of Xingu River, Brazil. Photo: J. Zuanon.

(Bottom right) The needlefish *Potamorrhaphis guianensis* staying motionless near the marginal vegetation in Araguaia River, Brazil. Needlefishes usually ambush small fishes and catch drifting invertebrates along river and lake banks. Photo: E. Ferreira.

substrate (Goulding and Ferreira, 1984), whereas groups of the widespread catfish *Pimelodus blochii* forage on a variety of food items that include fruits, invertebrates, fishes and organic debris. *Zungaro zungaro,* one of the giant pimelodid catfishes stays in the deeper portions close to the banks where it preys on medium-sized fishes, such as the migratory prochilodontids *Prochilodus* and *Semaprochilodus* (Goulding, 1979, 1980; Barthem and Goulding, 1997; authors' pers. obs.).

During the dry season, a large portion of the river margins appears in the form of sandy or muddy beaches (Plate 1.1). These gently sloping margins may form long extensions of shallow waters and represent rather simple habitats, with plenty of light scattered by the sand and clay particles suspended in the water. The highly seasonal nature of the beaches and its low structural complexity are supposed to result in rather unpredictable species assemblages (e.g. Goulding *et al.,* 1988; Ibarra and Stewart, 1989; Jepsen, 1997). Nevertheless, some field evidences indicate that the presence of a few "core species" that are rather frequent and numerically dominant in the fish fauna of the beaches. These species can be characterized by their small to medium size, drab and light color, and generalized feeding habits. Up to one hundred species of small characins, hemiodontids, loricariinae catfishes, shoaling engraulidids and cichlids (mostly geophagine "earth-eaters") comprise most of the fish fauna that congregate in the shallow beaches in the Amazon. Streamlined piscivorous characins such as species of *Acestrorhynchus, Boulengerella, Rhaphiodon vulpinus* and *Cynodon* patrol the open waters pursuing small fishes. Needlefishes (mainly *Pseudotylosurus* sp.) also hunt for small fishes close to the surface, biting off the head of their prey in the process (Goulding and Carvalho, 1984). The plain and well-lit sandy beaches are home to several hemiodontid fishes, such as *Argonectes longiceps, A. robertsi, Hemiodus immaculatus,* and *Bivibranchia* spp., that take mouthfuls of substrate and sift the insect larvae, microcrustaceans, and any small edible particles found among the sand. The odd-looking freshwater flatfishes *Hypoclinemus mentalis* and *Apionichthys* spp. (Achiridae) occupy the same habitat, burying themselves in the substrate in order to ambush invertebrates and small fishes.

Another group of fishes commonly found in the beaches are the scale-eaters. Several species of the characid genera *Roeboides, Roeboexodon, Bryconexodon, Exodon* and the wimple piranha *Catoprion mento* ambush their prey close to the shore, hidden from their prospective prey among submerged tree branches or grass leaves. Some scale eaters of the genus

Roeboides are supposed to rely on their body translucency and scattered light in the beaches to avoid being detected by their prey (Sazima and Machado, 1982), while others like *Exodon paradoxus* (Plate 1.1) are boldly marked and forage unobtrusively in large schools (Sazima, 1983).

At night-time a different set of fishes emerge from deeper river portions to forage in the shallow beaches, including predators that approach the shore to hunt for fish and other preys. The large and flat-headed pimelodid catfishes *Sorubimichthys planiceps, Pseudoplatystoma fasciatum* and *P. tigrinum* forage solitarily in the shallows, engulfing their prey (mainly resting diurnal fishes) with a loud, shot-like noise. Species of *Potamotrygon* stingrays (Plate 1.1) dig the soft substrate with their undulating pectoral fins in search for buried worms and insects, while large *Paratrygon aiereba* stingrays (up to 1.1 m disk diameter and over 70 kg) chases the resting diurnal fishes in the shallows. Long, flat-bodied and cryptic-colored loricariinae catfishes (e.g. *Loricariichthys* spp., *Loricaria* spp., *Pseudoloricaria laeviuscula)* that stayed partially buried in the substrate during the day emerge in the dark to feed on organic detritus and small insect larvae.

Although small fishes constitute one of the main prey items at night in the beaches, medium to large-sized fishes resting in the shallows are not safe either. Some highly specialized predators, the strictly hematophagous catfishes of the genus *Vandellia* (Trichomycteridae) (Plate 1.1) abound in some places, and feed on the blood of their host by piercing its arteries at the corner of branchial arches (Zuanon and Sazima, 2004a). The beach-dwelling Stegophilinae trichomycterids *Pseudostegophilus nemurus, Henonemus punctatus* and *Stegophilus* spp. are also highly specialized feeders. They apparently subsist exclusively on the mucus and scales of other fishes (Winemiller, 1989) that are rasped off by attaching the mouth to the host's body and widely swinging its body like a pendulum.

The river channels are supposed to serve mainly as migration routes for several groups of fishes, notably the long-ranging pimelodid goliath catfishes of the genera *Brachyplatystoma* (Junk *et al.,* 1989; Lundberg and Akama, 2005), as well as passive dispersion pathways to larval stages of many fish species. In fact, few fish species permanently inhabit the water column of the main river channel. Large individuals of the pristigasterid *Pellona castelnaeana* represents one of the few fishes that live in the open waters of white water river channels, pursuing smaller prey fishes (Le Guennec and Loubens, 2004). Some species of wide-mouthed catfishes of the genus A*geneiosus* also live in the river channels and hunt at night for fishes and shrimps that are gulped down whole.

The deeper portions of the river channels present a very distinct situation, with a high diversity of fishes living permanently in the dark river bottom. This fish fauna is composed mainly by catfishes (especially pimelodids, doradids, and loricariids) and by gymnotiform electric knife fishes (Lundberg et *al.,* 1987). The deep river channels do not sustain an important autochthonous primary productivity since light penetration is scarce and never reaches the bottom. The food utilized by the fishes is carried by the current from upstream locations after being produced in the lakes or in the flooded forests. Most of the fish fauna is composed by opportunistic foragers that depend on small animals, plant debris, organic detritus and even carcasses brought by the current to feed. The whale catfishes C*etopsis coecutiens* and C. *candiru* (Cetopsidae), and *Pareiodon microps* (Trichomycteridae) are examples of voracious carrion-feeders that forage on dead (or dying) animals in very large groups (just like the well-known piranhas in lakes). A high diversity of pimelodid catfishes (e.g. *Platystomatichthys sturio, Exallodontus aguanai, Aguarunichthys inpai, Propimelodus eigenmanni)* live permanently in the river channels and feed on animal matter (invertebrates, small fishes, and carrion) but their trophic interrelationships are largely unknown.

The diets and trophic relations of the gymnotiform knife fishes, which show an impressive variety of snout sizes, mouth shapes and teeth arrangements, remains scarcely studied. Some long-snouted species (e.g. *Sternarchorhynchus* spp. and *Sternarchorhamphus muelleri,* Apteronotidae) feed on insect aquatic larvae taken from small holes and channels in the mud bottom, in sponge beds or in conglomerates of pebbles or laterite (Marrero and Winemiller, 1993). One of the most bizarre feeding habits among knife fishes is shown by *Magosternarchus duccis* and M. *raptor* that seem to include the tail of other gymnotiform fishes as a staple item on their diets (Lundberg *et al.,* 1996). Despite such pinpointed examples, much remains to be studied about the trophic relationships of the deep channel fish assemblages of Amazonian rivers.

Floodplain Lakes

Among the different habitats recognized in the floodplain lakes, some are available throughout the year such as the open waters and the lake bottoms, whereas others are highly seasonal, like the floating meadows and flooded forests. The open waters are dominated by wandering predators and plankton-eating schooling fishes. Among the commonest predators are the clupeiform *Pellona flavipinnis* and the characiforms *Acestrorhynchus falcirostris* and A. *microlepis,* which pursue small fishes (mainly young-of-the-year of medium to large-sized species) in the water column. The fish- and invertebrate-eating *Ilisha amazonica* (Pristigasteridae) also forages in open water, where it feeds on small schooling engraulidid fishes (e.g. *Anchoviella* spp.), pelagic shrimps *(Acetes paraguayensis,* Sergestidae), and swimming insects like notonectid bugs (Heteroptera) and mayfly larvae (Ephemeroptera). Its large and dorsally positioned eyes possibly allow the capture of fishes and invertebrates that swim close to the surface, detected from bellow and evidenced against the sky light (JZ, pers. obs.).

Planktivorous fishes compose another feeding guild that forage in the open waters of lakes. Large schools of the pelagic catfish *Hypophthalmus* spp. (Pimelodidae) swim in the water column filtering mostly zooplankton (Carvalho and Goulding, 1985). Similarly, schools of the hemiodids *Anodus elongatus* and *Hemiodus* spp. consume mainly phytoplankton (although the later also frequently browse on periphyton). Some cichlids are also specialized plankton feeders, notably *Chaetobranchus flavescens, C. semifasciatus* and *Chaetobranchopsis orbicularis.* Close to the lake margin, small characids (mainly *Moenkhausia intermedia, Hemigrammus* spp., and *Tetragonopterus* spp.) feed on plankton and insects fallen in the water. The truly omnivorous *Triportheus albus, T. angulatus* and *T. elongatus* also scan the water surface searching for insects, small flowers, seeds of aquatic grasses, fruits, and organic debris carried by the wind or by the waves.

The lake bottom presents low dissolved oxygen content throughout most of the hydrological cycle. This oxygen depletion results from the microbial decomposition of large amounts of organic matter that accumulates in the bottom, and limits the presence of numerous fish species. The fish fauna in the lake bottom is dominated by air-breathing detritivorous loricariids, mainly species of *Liposarcus* and *Hypostomus,* and by the ubiquitous callichthyid catfish *Hoplosternum littorale* that feeds heavily on chironomid larvae. Huge schools of curimatids, notably *Psectrogaster rutiloides* (but also species of *Potamorhina, Curimata* and *Cyphocharax)* feed on the organic detritus at the lake bottom (Bowen, 1984; pers. obs.).

The floodplain lakes of white water rivers are fringed by a wide and dense carpet of aquatic and semi-aquatic plants, mainly grasses of the genera *Echinochloa, Paspalum* and *Oryza* (Junk and Piedade, 1993). These floating meadows are probably the richest and most productive aquatic habitats in the Amazon, with an enormous diversity and abundance of invertebrates and algae associated to the submerged roots and stems (Junk, 1970, 1973). Although frequently hypoxic, these habitats harbor an abundant and rich fish fauna (Henderson and Hamilton, 1995; Crampton, 1996; Sánchez-Botero and Araújo-Lima, 2001; Petry *et al.*, 2003), and supposedly function as a predator-safer environment for small-size fishes (Kramer *et al.,* 1978; Junk *et al.,* 1987; Anjos *et al.,* 2008). Nevertheless, the floating meadows are frequently visited by the pirarucu *Arapaima gigas,* one of the largest freshwater fishes in the world and a generalized carnivore that eats fish, crabs and insects (EF, pers. obs.). The ability to breathe air allows the pirarucu to withstand the low oxygen conditions that predominate among the aquatic grasses (Kramer *et al.,* 1978).

The floating meadows can occupy circa 30% of the lake area (Goulding *et al.,* 2003), but surprisingly very few species feed directly on the grass leaves, stems and roots. The few exceptions include the leaf-eating giant doradid catfish *Lithodoras dorsalis* (but that also feed on fruits in the flooded forest), and the anostomids *Schizodon fasciatus* and S. *vittatus* (Santos, 1982). Other anostomids like *Rhytiodus microlepis* and *R. argenteofuscus* are known to browse on the fine grass roots during the flooding season (Santos, 1982). Although there is no explanation for the low direct consumption of all that plant matter, some authors argue that it represents a strongly seasonal resource, and during the dry season (when almost all floating meadows are gone) the fishes suffer from food scarcity. Nevertheless, fishes are known to withstand extended periods without food, relying on fat reserves accumulated during the favorable season (Junk, 1985).

The periphyton and invertebrates found among the submerged roots and leaves of the aquatic plants are taken as food by a large number of small fishes that live in this habitat, even in the scarce *Oryza* wild rice banks found in some black water lakes (Araujo-Lima *et al.,* 1986). The cichlids of the genus *Mesonauta* are one of the most common fish species living in the floating meadows, where they feed on algae, phytoplankton and small invertebrates such as Conchostraca and Ostracoda. Juvenile individuals of important commercially exploited food fishes of the genera *Colossoma, Triportheus, Brycon, Mylossoma, Semaprochilodus* and *Prochilodus* use this habitat for food and shelter during their first months of life. Small tetragonopterine characins such as the ubiquitous *Ctenobrycon hauxwellianus* also live among the aquatic grass beds, feeding on small arthropods and seeds. Catfishes are present in large numbers, including small mollusk- and insect-eating doradids (e.g. *Doras* spp., *Nemadoras humeralis,* and *Pterodoras granulosus;* Nelson *et al.,* 1999), the omnivorous auchenipterids *Parauchenipterus* spp. and the periphytivorous loricariids *Hypoptopoma gulare* and *Rineloricaria castroi* (JZ, pers. obs.). Needlefishes (mainly *Potamorrhaphis guianensis,* Belonidae; Plate 1.1) are commonly found near the lake margins and close to the aquatic plants, slowly moving just below the water surface in search of invertebrates that fall in the water; small fishes are also occasionally ambushed by needlefishes.

Deeply inside the oxygen-depleted, compact dead grass mats that form in lakes is, the home of snake-like fishes such as swamp eels *(Synbranchus* spp.) and electric knife fishes (Gymnotiformes). Species of *Brachyhypopomus* (Hypopomidae) and *Eigenmannia* (Sternopygidae) feed on small aquatic invertebrates, whereas the larger *Sternopygus* spp. (up to 40 cm long) includes small fishes as an important item on its diet. The very large (up to 2 m long) electric eel *Electrophorus electricus* may also be found in those places, hunting for fishes that are knocked-out by its powerful electric shocks. The lungfish *Lepidosiren paradoxa* (Dipnoi: Lepidosirenidae) is also commonly found amidst the rotten grass beds, eating snails, insects and probably small fishes. The prey are brought to the lungfish's mouth by a powerful suction, and immediately smashed and crushed with its impressive set of fused teeth. Other fishes present in the rotten grass beds include mainly hypoxia-tolerant species like the predacious erythrinid *Hoplias malabaricus* (a fish and insect eater), young pacus of the genus *Mylossoma* (that forage in the periphyton for algae, microcrustaceans and insect larvae; Leite and Araujo-Lima, 2000, 2002), and cichlids like the invertebrate feeding *Cichlasoma amazonarum* (Ferreira, 1981; Sánchez-Botero and Araujo-Lima, 2001).

Flooded Forests

The seasonally available environment of the flooded forests represents a keystone in the ecology of some large, commercially important food fishes in the Brazilian Amazon (Gottsberger, 1978; Goulding, 1979, 1980; Kubitzki and Ziburski, 1994; Piedade *et al.,* 2003). The flooded forests of black water rivers are locally named 'igapós', and that of white water rivers as 'várzea' forests. These amphibious forests occupy an area of circa of 30% of the floodplains in Brazilian Amazon (Goulding *et al.,* 2003), and represent an important pathway for the allochthonous primary production to the aquatic environment.

The best examples of such fish-forest interaction are the large pacus and several piranha species (Characidae, Serrasalminae), and at least two large doradid catfishes, *Lithodoras dorsalis* and *Pterodoras granulosus* (Goulding, 1980). The tambaqui *Colossoma macropomum,* one of the main target fish species of the Amazon fisheries, depends largely on the fruits and seeds produced in the flooded forests to survive (Waldhoff *et al.,* 1996). The fruits and seeds that fall in the water are readily consumed by the tambaqui (Plate 1.1), including hard-shelled palm fruits that are broken by the fish's powerful jaws and cheek muscles (which exhibit a remarkable crushing power of up to 200 kg cm^{-2}; Araůjo-Lima and Goulding, 1997). Aside from its role in the energy transfer between the terrestrial and aquatic habitats, the tambaqui and several other fishes (e.g. *Triportheus* spp., *Brycon* spp., *Mylossoma* spp., *Parauchenipterus* spp., *Auchenipterichthys* spp., *Lithodoras dorsalis, Pterodoras granulosus)* may act as seed dispersers for many plant species of the flooded forests, thus contributing to the maintenance of its plant species diversity (Gottsberger, 1978; Goulding, 1980; Kubitzki and Ziburski, 1994; Ferreira, 2000; Mannheimer *et al.,* 2003; Piedade *et al.,* 2003). Piranhas such as the large and ferocious looking *Serrasalmus rhombeus* (up to 40 cm total length and 2 kg) also feed heavily on seeds in the flooded forests, but represent mainly a seed predator since it masticate most of the food consumed (pers. obs.).

The trophic relations in the flooded forests are not restricted to the fruits and seeds consumption by the fish fauna. Invertebrates that seek refuge from the floods in the vegetation also fall in the water and are readily consumed by many fish species such as *Brycon* spp., *Triportheus* spp., *Chalceus* spp., and many small to medium-sized characins during the day, and by *Auchenipterichthys* spp. and small cetopsids at night. Other species like the arrowanas *Osteoglossum bicirrhosum* and *O. ferreirai* even jump out of the water (sometimes up to two meters high) to reach large insects or spiders hanging from tree branches (Smith, 1979; Aragão, 1984; Goulding, 1989). Furthermore, the prochilodontids *Semaprochilodus* spp. and *Prochilodus* spp. enter the flooded forest to browse the periphyton growing on the submerged tree trunks, which represents a very important food source in the oligotrophic black water systems (Ribeiro, 1985).

The relationships between fishes and flooded forests probably represent the most remarkable biological interaction in the aquatic environments of the Amazon, but not only for its ecological significance. The huge amount of fruits and seeds that are produced during the flooding season sustains an equivalently large biomass of commercially valuable fishes, which enhances its importance as an energy pathway and for the regional fisheries (Araújo-Lima *et al.,* 1998). The knowledge of these intricate ecological interactions and their impact on the regional economy may represent an effective way to preserve the magnificent flooded forests and the amazing diversity of aquatic environments in the Amazon.

FOREST STREAMS: HIGH DIVERSITY IN A FOOD-LIMITED ENVIRONMENT

The Amazon forests are drained by an endless number of small streams of clear and black waters (Plate 1.2). Despite being unnoticed under the dense forest canopy that covers most of the region, these hidden watercourses contribute with a large portion of the water that the mighty Amazon River empties every year in the Atlantic Ocean (Goulding *et al.,* 2003). These streams help to maintain the typical high levels of relative humidity inside the forest and so conditioning the presence of very characteristic plant assemblages in the stream valleys (Ribeiro *et al.,* 1999).

The smallest water courses that drain the upland forests in the Amazon are first- to third-order streams which do not exhibit the seasonal flood pulse that dominate the dynamics of the large river-floodplain systems (Junk *et al.,* 1989). Instead, these streamlets show unpredictable floods of short duration (from some hours to a few days), dispersed along the lengthy Amazonian rainy season. This unpredictability does not allow for the development of the remarkable feeding specializations based on the consumption of fruits and seeds, as recorded in the floodplain habitats (Goulding, 1980). Nevertheless, the small and shallow forest streams harbor temporally stable, well defined fish assemblages.

These streams are characteristically oligotrophic (i.e., with a low autochthonous primary productivity) and apparently sustain a low biomass of fishes (e.g. Henderson and Walker, 1986; Walker, 1987; Silva, 1993; Mendonça *et al.,* 2005). Most of the time the sunlight barely reaches the stream surface, and the very low levels of nutrients in the water contribute to impair the growth of aquatic plants of almost all sorts (with the exception of some red algae species of the genus *Batrachospermum;* JZ,

Plate 1.2

(Upper left) General view of a typical forest stream, showing the clear water, predominantly sandy substrate and dense canopy cover. Photo: L.N. Carvalho.

(Upper right) The ubiquitous forest stream dweller *Pyrrhulina brevis* (Characiformes: Lebiasinidae) photographed in a field aquarium. Photo: F.P. Mendonça.

(Second row, left) Cryptically colored suckermouth armored catfishes like *Rineloricaria heteroptera* (Siluriformes: Loricariidae) graze the periphyton that grows attached to trunks, submerged roots and scarce macrophyte stands in forest streams. Photo: J. Zuanon.

Plate 1.2 Contd.

pers. obs.). Nevertheless, a single third-order stream, approximately 5 m wide and 1 m deep, may contain up to 50 fish species of five different orders (Anjos, 2005; Mendonça *et al.,* 2005; JZ, pers. obs.). Just to allow a comparison, this species richness corresponds to one fourth of the whole European freshwater fish fauna and ca. 10% of the freshwater fishes of North America (Goulding *et al.,* 2003).

The fish fauna of the small Amazonian streams is seemingly composed of a process of species addition from the headwaters to the larger water courses (Vannote *et al.,* 1980). The nutrient-limited environment of the first-order streams is occupied almost exclusively by fishes that feed on allochthonous sources of food, such as terrestrial insects and other small invertebrates that fall from the trees. Ants and termites are common food items in the stomach contents of these stream fishes and are caught as soon as they reach the water surface. The Gasteropelecids *Carnegiella strigatta* (Plate 1.2) and *C. marthae,* and the Characid *Gnathocharax steindachneri* have mastered this strategy aided by their upturned mouths and powerful pectoral fins, which allow a really fast access to the food that fall in the water surface. Small invertivorous such as the characins *Hemigrammus pretoensis* and *Hyphessobrycon agulha,* as well as the lebiasinids *Pyrrhulina brevis* (Plate 1.2) and *Copella nigrofasciata* figure among the most abundant fish species in the headwater streams in Brazilian Central Amazon. Although insects constitute the dominant food item in the diet of most species in these streams, the use of diverse feeding tactics, different foraging grounds and activity periods (day vs. night) allow for the coexistence of several fish species with similar diets (e.g. Soares, 1979; Silva, 1993; Sabino and Zuanon, 1998).

Plate 1.2 Contd.

(Second row, right) The catfish *Mastiglanis asopos* (Siluriformes: Heptapteridae) performing the drift trap foraging tactic during the night at the stream bottom. Photo: J. Zuanon.

(Third row, left) A small group of the dwarf cichlid *Apistogramma hyppolitae* (Perciformes: Cichlidae) sifting the detritus layer that accumulates in the litter banks for edible particles and invertebrates. Photo: J. Zuanon.

(Third row, right) An adult *Rivulus compressus* (Rivulidae: Cyprinodontiformes) camouflaged among the leaf litter in a desiccating pond at Reserva Florestal Adolpho Ducke, Manaus, Amazonas State, Brazil. Photo: J. Zuanon.

(Bottom left) The powerful pectoral fins of the marbled butterfly fish *Carnegiella strigata* (Characiformes: Gasteropelecidae) allow the fish to quickly reach allochthonous invertebrates fallen at the water surface. Photo: J. Zuanon.

(Bottom right) The traira or wolf characin *Hoplias* cf. *malabaricus* (Characiformes, Erythrinidae), a top predator in small streams, ambushes its prey among submerged plants. Photo: J. Zuanon.

Reduction of body size (= miniaturization; Weitzman and Vari, 1988) seems to constitute a very common trait among fishes that inhabit food-limited environments. In fact, one of the few recognizable common characteristics of stream fishes in Brazil is the small adult size of most species (up to 15 cm standard length; Castro, 1999). This condition is also observed in the black waters of the enormous Negro River, where nutrients and, ultimately, food are very scarce in the aquatic environment. The low primary productivity and scarcity of food are expectedly reflected in the stream trophic chain, where detritivorous fishes are rare to almost absent. The trophic link between the producers and the ichthyofauna is through the leaf-processing invertebrates, which constitute an important food source for many fish species.

The food chain in forest streams is characteristically simple and short (Walker, 1987). The mentioned rarity of detritivorous fishes is accompanied by the inexistence of phytoplanktivorous and strictly zooplanktivorous species. As already mentioned, the low light and nutrient-poor waters of the forest streams do not sustain large enough populations of planktonic algae and microcrustaceans to allow for the existence of plankton-feeding specialists. Similarly, the almost absence of aquatic macrophytes impairs the occurrence of plant (leaf) eating fishes. So, among the fishes that inhabit forest streams the primary consumers are mainly represented by periphytivorous loricariids of the genera *Rineloricaria, Acestridium, Farlowella, Ancistrus* and *Parotocinclus*. The most abundant loricariids in the forest streams seem to be species of *Rineloricaria,* especially *R. lanceolata* and *R. heteroptera* (Plate 1.2). These species are usually found at stream stretches where the forest canopy is somewhat open, so allowing the presence of stands of bog plants like *Thurnia sphaerocephala* (Thurniaceae), where the suckermouth catfishes graze the periphyton that grows in the leaf blades.

Other fish species inhabit the slow-flowing stream margins, taking advantage of the calmer conditions to browse on algae and nip on associated tiny invertebrates along the clay banks and on submerged trunks and tree branches. These micro-omnivorous fishes are represented by some *Nannostomus* species, notably the beautiful and widespread *N. marginatus* in the smaller streams. In streams of third order and up, this niche is frequently occupied by some cichlid species of the genus *Mesonauta,* the ubiquitous Amazonian flag cichlid. The streamlined characins *Iguanodectes variatus* and *I. geisleri* are also frequently observed browsing on algae attached to thin tree roots that emerge from the banks and from the stream bottom, making conspicuous head-twisting movements while foraging.

Mainly invertivorous fishes that feed on allochthonous insects, spiders, mites and invertebrates, as well as immature aquatic insects compose the secondary consumers. This trophic group commonly includes several characiform fishes (e.g. species of *Bryconops, Hyphessobrycon, Hemigrammus, Moenkhausia, Poptella, Axelrodia, Pyrrhulina, Copella* and others) and perciforms (mainly cichlids of the genera *Apistogramma* and *Aequidens),* as well as the siluriforms *Helogenes marmoratus* and *Denticetopsis seducta* (Cetopsidae), *Tatia* spp. (Auchenipteridae), *Ituglanis amazonicus* (Trichomycteridae), *Mastiglanis asopos* and *Brachylanis* cf. *microphthalmus* (Heptapteridae). The presence of several species of fishes exploring the same kind of food resource may seem contradictory in an oligotrophic environment. This situation seems to be allowed by some sort of resource sharing, and the activity period (diurnal vs. nocturnal) is possibly the most common and simple way to accomplish this. Characins and cichlids compose the majority of the diurnally active fishes in the forest streams, whereas the night-time is dominated by catfishes (Siluriformes) and knifefishes (Gymnotiformes) (Lowe McConnell, 1987). Nevertheless, some fishes exhibit a higher trophic specialization and feed on fewer prey types. This is the case of the Auchenipterid *Tetranematichthys quadrifilis,* which eats mainly shrimps and constitute one of the few carcinophagous (crustacean-eating) fish species in the Amazon (although insects may be occasionally preyed on by the catfish).

Another form of resource sharing includes the vertical stratification of foraging grounds. Several fishes feed on aquatic invertebrates that live over and amidst the sandy bottom of the streams. During the day, generalized sit-and-wait foragers like species of the genus *Characidium* (Crenuchidae) exploit the bottom dwelling and drifting invertebrates along the shallow stream margins. In fast-flowing stretches, the minute ghost candiru *(Stauroglanis gouldingi,* Trichomicteridae) feeds on very small aquatic insect larvae and harpacticoid copepods that accumulate in the grooves formed behind sand ripples (Zuanon and Sazima, 2004b). At night, the sit-and-wait invertivorous niche is occupied by the heptapterids *Imparfinis pristos* and *Mastiglanis asopos* that feed on drifting prey while poised on the stream bottom surface (Plate 1.2). Species of the sand knifefish *Gymnorhamphichtys* forage by probing the upper layer of the sand with their tubular snouts where they prey on small chironomid (bloodworm) larvae and harpacticoid copepods (Zuanon *et al.*, 2006). In larger streams, species of *Satanoperca* and *Geophagus* (Cichlidae) sift food from the bottom by taking a mouthful of substrate and sorting the edible portions (aquatic invertebrates, organic particles) in the oral chamber. Finally, the minute, eel-like trichomycterid species of the genus *Pygidianops* goes deeper and literally 'swims' amidst the sand searching for tiny aquatic invertebrates, and apparently never ventures out of its cover (Schaefer *et al.,* 2005; JZ, pers. obs.).

The litter banks are also shared by several fish species of different groups. The dwarf cichlids of the genus *Apistogramma* seek shelter and forage on the upper layer of the banks, picking up small aquatic invertebrates and sifting through small amounts of organic detritus during the day (Plate 1.2). At night, the widespread banjo catfishes of the genus *Bunocephalus* (such as B. *coracoideus* and *B. verrucosus,* Aspredinidae) forage by slowly moving over the leaf substrate pushed by jets of water expelled through the gill openings. Insect larvae and other small aquatic invertebrates are found with the use of its barbels and quickly sucked from the substrate. Another common inhabitant of the litter banks is the crenuchid *Elachocharax pulcher* (as well as the occasionally syntopic *E. mitopterus* and *E. junki);* surprisingly, these small characiforms (up to 20 mm SL) are nocturnal but very little is known about its ecology. The eel-like fishes that occupy the muddy and hypoxic deeper layers complete the vertical stratification of the litter banks. The swamp eels of the genus *Synbranchus* are commonly found under these conditions, along with electric fishes of the genera *Gymnotus, Microsternarchus, Hypopygus* and *Brachyhypopomus* (Gymnotiformes). Although little information is available about the natural history of these species, it seems that most of them leave the litter banks at night to forage in open waters for small fishes and aquatic invertebrates. But analogous to the sand-diving *Pygidianops* trichomycterids in the sand banks, the red-bodied heptapterid species of the genus *Phreatobius* keeps deep inside the litter banks, moving amidst the thick packs of dead leaves and (supposedly) feeding on minute invertebrates (Muriel-Cunha and de Pinna, 2005; JZ, pers. obs.).

The top predators among the forest stream fishes are represented mainly by the wolf characins of the Family Erythrinidae (Géry, 1977). In the smaller (first- and second-order) streams, the most abundant carnivore is the 'jeju' *Erythrinus erythrinus,* a fish that attains ca. 15 cm SL and feeds on small fishes and insects. The larger *Hoplerythrinus unitaeniatus* and *Hoplias* cf. *malabaricus* (Plate 1.2) stand among the most common and abundant crepuscular to nocturnal fish predators in the larger streams, as well as in several South American water bodies. Juvenile specimens of the piscivorous *Rhamdia* catfishes (Heptapteridae) may be occasionally found venturing upstream in small forest streams, whereas the wide-mouthed *Batrochoglanis raninus* (Pseudopimelodidae) is frequently found in the crevices of submerged logs lurking for prey fishes at night. During the day, individuals of the dogtooth characin *Acestrorhynchus falcatus* (Acestrorhynchidae) cruises at mid water pursuing small tetras (Characidae) in second order and larger streams.

Temporary Ponds along the Streams: To Eat or to be Eaten?

During the rainy season, several ponds may be formed in flat-bottomed valleys along the forest streams. Although insects and frogs are the main colonizers of the ponds, these small and (usually) ephemeral environments are also capable of sustaining a particular assemblage of fishes that differs from a simple subset of the stream ichthyofauna. It is supposed that the marginal ponds constitute a more productive environment for the growth of larvae and juvenile fish, like the floodplain lakes associated to larger rivers. In fact, a large portion of the fishes found in marginal ponds of forest streams in Central Amazon is composed by juvenile specimens (Pazin *et al.,* 2006). Nevertheless, some fish species are far more common in ponds than in the stream channels, and there are trophic differences among these habitats.

The ponds are colonized mainly by means of opportunistic migrations of fishes during the sporadic floods of the streams. In other instances, some air-breathing species actively migrate through runoff waters or even moist land to the nearby ponds. This group of species includes the predatory characiforms *Erythrinus erythrinus* and *Hoplias* cf. *malabaricus,* the siluriforms *Callichthys callichthys* and *Megalechis thoracata,* and the cyprinodontiform *Rivulus compressus.* The most obvious advantage of being the first colonizers is the access to newly available food sources and shelter. Aquatic immature insects like bloodworms (Diptera, Chironomidae), leaf-cased caddis fly (Trichoptera) and microcrustaceans (mainly Ostracoda and Cladocera) readily colonize the ponds and are heavily consumed by the fishes. On the other hand, the highly predatory dragonfly nymphs (Odonata) also figure among the earlier colonizers but attracted by the predictable abundance of food.

The trophic chain in the ponds seems to be slightly different from that in the stream channel. The ubiquitous *Pyrrhulina brevis* and *Copella nigrofasciata* again constitute a large portion of the fishes foraging on insects and other invertebrates that fall into the water surface. Several *Rivulus* species (mainly *R. compressus* in the Central Amazon; Plate 1.2) occupy the uppermost layer of the ponds, staying almost motionless at the surface and close to the pond margin, preying chiefly on small ants. Small cichlids (mainly *Apistogramma* and juvenile specimens of *Aequidens pallidus)* and the beautiful crenuchid *Poecilocharax weitzmani* feed on small aquatic invertebrates among the leaf litter that accumulates in the pond bottom. The callichthyids *Megalechis thoracata* and *Callichthys callichthys* also forage on the bottom, probing the substrate with their barbels and feeding on a compound of organic particles and associated micro-invertebrates, thus inserting a detritivorous component in the food chain. Again, the main piscivorous fishes in this aquatic habitat are the erythrinids and *Synbranchus*, which seems to be very efficient predators in the shallow, leaf-packed environment of the ponds.

Although more productive and (supposedly) less competitively stressful than the stream channel, colonizing the marginal ponds present some risks to the survival of the fishes. The main problem is related to the survival during the dry season, when most of the ponds dry completely and may turn into a deadly seasonal trap. Evading the ponds at the end of the rainy season and just before they become completely isolated from the stream seems to be the commonest strategy employed by opportunistic occupants of the ponds, like most of the small characins. The disconnection from the stream does not represent a problem for the air-breathers *Callichthys* and *Megalechis,* which can migrate back to the channel by dry land. A similar emergency escape strategy is shown by species of *Rivulus* that just jump away from the ponds to the stream (although *R. compressus* can withstand the dry period partially buried in the mud or moist leaf litter). The leaf-litter specialists like the eel-like *Phreatobius* catfishes can migrate to deeper layers of the litter bed where some water (or moister conditions) remains throughout the dry season. Some electric fishes (several species of *Gymnotus)* and swamp eels *(Synbranchus)* can bury themselves and survive the desiccation of the ponds inside the muddy bottom or in moist galleries. During that time, these species do not eat and survive on the fat reserves accumulated along the rainy season. Annual killifishes that specialize in ephemeral environments and complete the short (less than a year) life cycle in the pond (by means of burying the eggs in the soft pond substrate) are not common in the forest environments of the Central Amazon.

As mentioned before, the productive environment of the marginal ponds may turn in a very risky environment for fishes, since they are occupied by some large and voracious predators like *Pipa* toads (Pipidae) and the small fish-eating twist-necked turtle *Platemys platycephala* (Chelidae). Furthermore, the desiccating ponds frequently end up with reversed predator-prey roles in the food chain: invertebrates as predators (mainly dragonfly larvae and giant water bugs of the family Belostomatidae), and vertebrates as prey (fishes and amphibian larvae). In conclusion, the different abilities of fish to stand in such an ephemeral habitat play a major role in the constitution of fish assemblage in ponds, which may change along time as a result of the complex interactions among predators and prey in that aquatic environment.

RAPIDS AND WATERFALLS: GRAZING ROCKS FOR A LIVING

Besides the huge floodplains and the lengthy white water rivers that form the dominant elements in the region, the Amazon Basin comprises other aquatic environments that harbor some specialized assemblages of fishes. A very different kind of aquatic habitat exists in the region where the Amazon's sedimentary floodplain contacts the Guyana and the Central Brazilian Plateaus. These transition zones are far from smooth: there, a series of rapids and waterfalls clearly mark the limits of two very different aquatic environments. Downstream from the rapids these rivers show a predictable annual flood pulse that strongly influences the dynamics of the rivers themselves and of their fish fauna. Upstream the riffle zone the landscape is composed by a long stretch of rocky outcrops and turbulent waters, where stands of podostemaceans plants carpet the rocks under the strongest water flow.

Most of the rapids and waterfalls located at the edge of the two main plateaus are formed by clear water rivers that carry very few suspended solids, since they drain very old, continuously washed granitic rocks (Plate 1.3). Although clear water rapids constitute the more common situation in the Brazilian Amazon, rapids zones also occur in rivers of different water

Plate 1.3

(Upper left) General view of some rapids in the Xingu River near the city of Altamira, Pará State, Brazil. Note the clear water typical of most rivers that drain the Central Brazilian plateau. Photo: J. Zuanon.

(Upper right) The underside of submerged rocks in Xingu River is colonized by several numerous invertebrates like sponges, gastropods, and insect larvae that are utilized as food by several rapids-dwelling fishes. Photo J. Zuanon.

Plate 1.3 Contd.

types. Black water rapids exist in the upper reaches of the Negro River near the Brazilian-Colombian border and in a few other tributaries. White water rapids and waterfalls are extremely rare: they occur only in the Madeira River, extending from the vicinity of Porto Velho (Rondônia State) upstream to the Bolivian border. Both black- and white-water rapids harbor a lower diversity of strictly rheophilic fishes when compared with clear water rivers (JZ, pers. obs.), which seems to result from differences in the local primary productivity. In black waters, the light penetration is limited by the large amount of dissolved organic matter that darkens the water and impairs the growth of periphyton in the submerged rocks (Goulding *et al.,* 1988). In white water rapids the light is scattered by the huge amount of suspended sediments carried by the Madeira River, and the incident light barely penetrates the upper (20 cm) layer of water (Goulding *et al.,* 2003). These facts indicate that food (periphyton) is probably the main limiting factor to the fish fauna in black and white water river rapids, although faunal limitations cannot be ruled out.

The rapids constitute highly structured habitats, where rocks of different sizes provide lots of shelters for fishes and other aquatic life. The hard rocky substrate allows for the establishment of a dense cover of algae and other sessile organisms like sponges, bryozoans and podostemaceans plants. Nevertheless, these characteristics are accompanied by a strong

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Plate 1.3 Contd.

(Second row, left) The zebra pleco *Hypancistrus zebra* (Siluriformes: Loricariidae) photographed in a field aquarium. The bold color pattern rendered this species very attractive to the aquarium trade, occasionally driving it to an endangered conservation status. Photo: J. Zuanon.

(Second row, right) A close-up view of *Sartor respectus* (Characiformes: Anostomidae) photographed in field aquarium just after capture in the Xingu River. Note the upturned mouth and the protruding red-tipped teeth that are employed to scrap off sessile invertebrates from submerged rocks. Photo: J. Zuanon.

(Third row, left) The riffle specialist anostomid *Leporinus julii* (Characiformes: Anostomidae) browsing the periphyton of submerged rocks in the Xingu River. Photo: J. Zuanon.

(Third row, right) Omnivorous generalists like *Leporinus* aff. *fasciatus* (Characiformes: Anostomidae) are commonly found foraging behind rocks and so protected from the direct action of the current. Note the dark sponges where the fish is feeding. Photo: J. Zuanon.

(Bottom left) The odd-looking pacu *Ossubtus xinguense* (Characiformes: Characidae: Serrasalminae) photographed just after capture. This endemic species of the Xingu River in Brazil feeds on algae and podostemacean plants that grow attached to the rocks in the rapids. Note its strongly down-turned mouth. Photo: J. Zuanon.

(Bottom right) The rapids-dwelling cichlid *Retroculus xinguensis* (Perciformes: Cichlidae) photographed just after capture. Note the long snout and thick lips that allow this species to forage deeply in sand-pebbles substrate of the rapids. Photo: J. Zuanon.

water turbulence that limits the presence of most of the fish species that abound in the calmer downstream sections of those rivers. To cope with these environmental conditions, several morphological, physiological and behavioral solutions have evolved in different fish groups.

The fish fauna in the clear water rivers rapids is characteristically rich and diverse. More than a hundred species may occupy a relatively short (100 km) stretch of the Xingu River rapids (Zuanon, 1999), and similar numbers may be found in the Tocantins, Trombetas and other rivers in the Brazilian Amazon (pers. obs.). This impressive species richness is apparently supported by the high primary productivity in the rapids, where periphyton constitutes the main food or foraging ground for the fish fauna. The diverse characteristics of the rocky substrate and water flow dynamics, coupled with the morphological diversity of the fishes, have allowed the coexistence of many fish species. The consumption of a same food type by so many fishes seems possible by the use of a variety of feeding tactics and behavioral traits.

Variations over a Theme: Mouth Morphology, Teeth Types and Trophic Characteristics of Rapids-dwelling Fishes

One of the most successful fishes dwelling in the rapids are the Loricariids or armored suckermouth catfishes. Although usually known as important detritivorous or periphytivorous, these odd-shaped catfishes are, in fact, versatile foragers that exploit a large diversity of food types. Loricariids use their sucker mouths and specialized teeth to graze on several kinds of food, which result in diverse feeding habits: detritivory, periphyitivory, omnivory, and even invertivory. Some loricariid species go even further and seems to show specialized carnivorous habits, feeding on hard-shelled invertebrates like mollusks and caddis fly larvae, and even sponges. This feeding tactic known as durophagy (Hoogerhoud, 1987; Turingan, 1994) is exhibited by members of the genus *Scobinancistrus,* which possess a few strong teeth that seem to be employed as pincers to scrap off food from the rocky surface. On the other hand, the flat-bodied *Ancistrus ranunculus* feeds on minute algae and cyanobacteria that seem to be obtained by suspending the fine detritus layer settled on the slit-like cracks on the rocks inhabited by these catfish (Müller *et al.,* 1994; Zuanon, 1999). The delicate and numerous teeth of *A. ranunculus* and other loricariids seem adequate to feed on loosely settled unicellular diatomaceous algae that grow amidst the firmly attached tufts of filamentous blue-green algae

(Cyanophyceae), by 'combing' the algae tufts (Müller *et al.,* 1994; Rapp Py-Daniel and Zuanon, 2005).

Although predominantly herbivorous, some loricariids include a significant portion of animal food in their diets. The boldly patterned catfish *Hypancistrus zebra* (Plate 1.3) seems to be a sedentary forager that explores small areas around its shelter on the rocks, where it feeds on periphyton, chironomid larvae and microcrustaceans. The 'v'-shaped dentary teeth of the zebra loricariid seem to allow the selection of small prey animals amidst the detritus layer or periphyton that cover the rocks. Finally, some species of loricariid shows a bizarre diet composed by wood fragments gathered from submerged trunks and logs. The wood-eating *Panaque nigrolineatus* and *Hypostomus cochliodon* scrap small pieces of wood aided by the strong and spoon-shaped teeth in both jaws, and are apparently capable of digesting the cellulose matter aided by symbiotic invertebrates living on their guts (Nelson *et al.,* 1999).

Scraping food from the rocks is also the main feeding strategy of a very different group of fish. The leporins and allies of the family Anostomidae are torpedo-shaped characiform fishes that abound in the rapids and constitute the more conspicuous inhabitants of the fast flowing rocky stretches of clear water rivers. The widespread *Leporinus friderici* and the boldly patterned *L. tigrinus* and L. cf. *fasciatus* (Plate 1.3) occupy the periphery of the rapids where they feed on a variety of invertebrates, algae and other organic debris. These species do not present evidence of morphological adaptations related to the life in the rapids and seem to occupy those habitats by means of a simple strategy: to avoid struggling against the faster, more turbulent waters of the rapids. These two species, as well as several fishes of various taxonomic groups use the patch of calmer waters formed downstream of rocks and other obstacles to occasionally access some feeding grounds in the middle of the rapids. A far more specialized way to avoid the direct effects of the currents is showed by *Sartor respectus,* a small anostomid species with an upwardly directed mouth (Plate 1.3). The very large dentary teeth of this fish emerge out of the mouth and are utilized to scrap off hard-bodied invertebrates (bryozoans, sponges) from the ceilings of dark shelters under the rocks (Santos and Rosa, 1998; Zuanon, 1999) (Plate 1.3). These fishes apparently do not venture out of their rocky shelters and probably constitute one of the more specialized species that inhabit the rapids stretches of clear water rivers.

Nevertheless, there are truly rheophilic specialists among the anostomids that live in the rapids. *Leporinus julii* (Plate 1.3) is a long and slender species that possess a down-turned mouth furnished with a series of aligned sharp teeth that allow it to browse and graze the algae that carpet the rocks in the shallow, faster flowing stretches of the rapids. The streamlined body allows the fish to roll on its sides and reach and graze on tufts of algae that grow in the small nooks and crannies of the rock surface. The thick margins of the pelvic, anal and lower lobe of the caudal fins are utilized as a tripod that helps the fish to hold position against the current while foraging.

Another group of Characiformes constitute an important component of the fish fauna in the rapids: the leaf-cutting and algae-browsing pacus (Characidae: Serrasalminae). Species of *Mylesinus* and *Tometes* occupy the stronger flowing stretches of the rapids, where they feed mainly on the leaves of podostemaceans plants that grow on the rock surface. A further step towards the life strictly in the rapids is shown by *Ossubtus xinguense,* which have a down-turned mouth and scraps algae in flat rocks at the bottom of the rapids (Plate 1.3). This endemic species of the Xingu River probably represents the most extreme example of morphological adaptation to the rheophilic life among the serrasalmines.

Although unexpectedly, some cichlids also inhabit the rapids of clear water rivers in the Amazon. The above-mentioned strategy of avoiding the direct effects of the strong currents is also employed by several species of *Crenicichla* that hunts for small fishes and aquatic invertebrates among the rocks at the bottom of rapids. Similarly, some peacock basses of the genus *Cichla* have been observed hunting for prey in the turbulent zone downstream of small waterfalls in Trombetas and Xingu rivers (pers. obs.). Nevertheless, some cichlids can be considered as strictly rheophilic. *Retroculus xinguensis* (Plate 1.3) digs the gravel and sand substrate in fast-flowing river stretches, where it feeds on chironomids, mayfly and caddis fly larvae (Moreira and Zuanon, 2002). The small pike cichlids of the genus *Teleocichla* also live in the rapids and feed on aquatic invertebrates (Zuanon, 1999). Of these, *Teleocichla centisquama* is a strongly rheophilic species that forages at the top of submerged boulders directly exposed to the strong water current, where it picks small insect larvae and micro crustaceans at the rock surface (Zuanon, 1999; Zuanon and Sazima, 2002).

After night fall, the bottom of the rapids is occupied by several carnivorous species that feed on fishes and aquatic invertebrates under the rocks, including small catfishes of the genera *Microglanis* (Pseudopimelodidae) and *Myoglanis* (Heptapteridae), and juvenile specimens of the swamp eel *Synbranchus* spp. (Synbranchidae). Some very large individuals of *Hoplias macrophthalmus* are frequently seen ambushing preys under rocky shelters in the rapids, and the weakly electric eel *Archolaemus blax* (Sternopygidae) emerges from small spaces and cracks in the rocks to forage for insect larvae and small fishes.

In conclusion, trophic relationships play a major role in the structure of fish assemblages in the rapids of Amazonian rivers. The high primary productivity, coupled with slight variations in mouth and teeth morphology and different feeding strategies, allow for the presence of a highly diverse fish fauna. The presence of many endemic species in the rapids also points out to the need for special conservation strategies since those areas are highly threatened by the construction of hydroelectric power plants in the Brazilian Amazon.

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References

Anjos, M.B. 2005. *Composição, distribuição e características tróficas da ictiofauna de igarapés de terra firme na Amazônia Central.* Unpublished M.Sc. Thesis. Instituto Nacional de Pesquisas da Amazônia/Universidade Federal do Amazonas, Manaus.

Anjos, M.B., R.R. Oliveira and J. Zuanon. 2008. Hypoxic environments as refuges against predatory fish in Amazonian floodplain. *Brazilian Journal of Biology* 68(1): 631-637.

Aragão, L.P. 1984. Contribuição ao estudo da biologia do aruanã, *Osteoglossum bicirrhosum* Vandelli 1829, do lago Janauacá - Estado do Amazonas, Brasil. 1. Alimentação na fase adulta. *Boletim de Ciências Agronômicas,* Fortaleza 17: 113-126.

Araujo-Lima, C.A.R.M. and M. Goulding. 1997. So fruitful a fish - *Ecology, Conservation and Aquaculture of the Amazon's Tambaqui.* Columbia University Press, New York.

Araujo-Lima, C.A.R.M., L.P.S. Portugal and E.J.G. Ferreira. 1986. Fish-macrophyte relationship in the Anavilhanas Arquipelago, a blackwater system in the Central Amazon. *Journal of Fish Biology* 29: 1-11.

Araujo-Lima, C.A.R.M., M. Goulding, B. Forsberg, R. Victoria and L. Martinelli. 1998. The economic value of the Amazonian flooded forest from a fisheries perspective. *Internationale Vereinigung fur Theoretische und Angewandte Limnologie* 26: 2177-2179.

Barthem, R. and M. Goulding. 1997. *The Catfish Connection.* Columbia University Press, New York.

Bowen, S.H. 1984. Detritivory in Neotropical fish communities. In: *Evolutionary Ecology of Neotropical Freshwater Fishes,* T.M. Zaret (ed.). Dr. W. Junk Publishers, The Hague, pp. 59-66.

Carvalho, M.L. and M. Goulding. 1985. On the feeding ecology of the catfish *Hypophthalmus fimbriatus* in the blackwater Rio Negro of the Amazon basin. *Revista Brasileira de Zoologia* 3: 33-41.

Castro, R.M.C. 1999. Evolução da ictiofauna de riachos sul-americanos: padrões gerais e possíveis processos causais. In: *Ecologia de Peixes de Riachos,* E.P. Caramaschi, R. Mazzoni and PR. Peres-Neto (eds.). Série Oecologia Brasiliensis, *Programa de Pós-graduação em Ecologia,* Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil, Vol. 6, pp. 139-155.

Claro Junior, L.H., E.J.G. Ferreira, J. Zuanon and C.A.R.M. Araujo-Lima. 2004. O efeito da floresta alagada na alimentação de três espécies de peixes onfvoros em lagos de várzea da Amazônia Central, Brasil. *Acta Amazonica* 1: 133-137.

Cox Fernandes, C., J. Podos and J.G. Lundberg. 2004. Amazonian ecology: tributaries enhance the diversity of electric fishes. *Science* 305: 1960-1962.

Crampton, W.G.R. 1996. Gymnotiform fishes: an important component of Amazonian floodplain fish communities. *Journal of Fish Biology* 48: 298-301.

Ferreira, E.J.G. 1981. *Alimentação dos adultos de doze espécies de ciclideos (Perciformes, Cichlidae) do rio Negro, Brasil.* Unpublished M.Sc. Thesis. Instituto Nacional de Pesquisas de Amzonia, Universidade Federal do Amazonas, Manaus.

Ferreira, E.J.G. 1993. Composição, distribuição e aspectos ecológicos da ictiofauna de um trecho do rio Trombetas, na área de influência da futura UHE Cachoeira Porteira, Estado do Pará, Brasil. *Acta Amazonica* 23: 1-88.

Ferreira, L.V. 2000. Effects of flooding duration on species richness, floristic composition and forest structure in river margin habitat in Amazonian blackwater floodplain forests: implications for future design of protected areas. *Biodiversity and Conservation* 9: 1-14.

Géry, J. 1977. *Characoids of the World.* T.F.H. Publications Inc., Neptune City, NJ.

Gottsberger, G. 1978. Seed dispersal by fish in the inundated regions of Humaitá, Amazônia. *Biotropica* 13: 170-183.

Goulding, M. 1979. *Ecologia da pesca no rio Madeira.* Instituto Nacional de Pesquisas de Amazonia, Manaus.

Goulding, M. 1980. *The Fishes and the Forest: Exploration in Amazonian Natural History.* University of California Press, Los Angeles.

Goulding, M. 1989. *Amazon - The Flooded Forest.* BBC Book, London.

Goulding, M. and M.L. Carvalho. 1982. Life history and management of the tambaqui *(Colossoma macropomum,* Characidae): An important Amazonian food fish. *Revista Brasileira de Zoologia* 1: 107-133.

Goulding, M. and M.L. Carvalho. 1984. Ecology of Amazonian needlefishes (Belonidae). *Revista Brasileira de Zoologia* 2: 99-111.

Goulding, M. and E.J.G. Ferreira. 1984. Shrimp-eating fishes and a case of prey switching in Amazon Rivers. *Revista Brasileira de Zoologia* 2: 85-97.

Goulding, M., M.L. Carvalho and E.G. Ferreira. 1988. *Rio Negro: Rich Life in Poor Water.* SPB Academic Publishing, The Hague.

Goulding, M., R. Barthem and E. Ferreira. 2003. *The Smithsonian Atlas of the Amazon.* Smithsonian Press, Washington.

Henderson, PA. and H.F. Hamilton. 1995. Standing crop and distribution of fish in drifting and attached floating meadow within an upper Amazonian várzea lake. *Journal of Fish Biology* 47: 266-276.

Henderson, PA. and I. Walker. 1986. On the leaf litter community of the Amazonian blackwater stream Tarumazinho. *Journal of Tropical Ecology* 2: 1-17.

Hoogerhoud, R.J.C. 1987. The adverse effects of shell ingestion for molluscivorous cichlids, a constructional morphological approach. *Netherlands Journal of Zoology* 37: 277-300.

Ibarra, M. and D.J. Stewart. 1989. Longitudinal zonation of sandy beach fishes in the Napo River basin, eastern Ecuador. *Copeia* 1989: 364-381.

Jepsen, D.B. 1997. Fish species diversity in sand bank habitats of a Neotropical river. *Environmental Biology of Fishes* 49: 449-460.

Junk, W.J. 1970. Investigations on the ecology and production biology of the "floating meadows" *(Paspalum-Echinochloetum)* on the middle Amazon. Part I: the floating vegetation and its ecology. *Amazoniana* 2: 449-495.

Junk, W.J. 1973. Investigations on the ecology and production biology of the "floating meadows" *(Paspalum-Echinochloetum)* on the Middle Amazon. Part I: The aquatic fauna in the root zone of floating vegetation. *Amazoniana* 4: 9-102.

Junk, W.J. 1985. Temporary fat storage, an adaptation of some fish species to the water level fluctuations and related environmental changes of the Amazon river. *Amazoniana* 9: 315-351.

Junk, W.J. 1997. *The Central Amazon Floodplain: Ecology of a Pulsing System.* Ecological Studies 126. Springer-Verlag, Berlin.

Junk, W.J. and M.T.F. Piedade. 1993. Herbaceous plants of the Amazon floodplain near Manaus: Species diversity and adaptations to the flood pulse. *Amazoniana* 12: 467-484.

Junk, W.J., M.G.M. Soares and F.M. Carvalho. 1987. Distribution of fish species in a lake of the Amazon river floodplain near Manaus (Lago Camaleão), with special reference to extreme oxygen conditions. *Amazoniana* 7: 397-431.

Junk, W.J., P.B. Bayley and R.E. Sparks. 1989. The flood pulse concept in river-floodplain systems. *Special Publications of the Canadian Journal of Fisheries and Aquatic Sciences* 106: 110-127.

Knöppel, H.A. 1970. Food of Central Amazonian fishes: contribution to the nutrient-ecology of Amazonian rain-forest-streams. *Amazoniana* 2: 257-352.

Kramer, D.L., C.C. Lindsey, G.E.E. Moodie and E.D. Stevens. 1978. The fishes and the aquatic environment of the central Amazon basin, with particular reference to respiratory patterns. *Canadian Journal of Zoology* 56: 717-729.

Kubitzki, K. and A. Ziburski. 1994. Seed dispersal in flood plain forests of Amazonia. *Biotropica* 26: 30-43.

Le Guennec, B. and G. Loubens. 2004. Biologie de *Pellona castelnaeana* (Teleostei: Pristigasteridae) dans le basin du Mamoré (Amazonie bolivienne). *Ichthyological Exploration of Freshwaters* 15: 369-383.

Leite, R.G. and C.A.R.M. Araujo-Lima. 2000. A dieta das larvas de *Mylossoma aureum* e *M. duriventre* na Amazônia Central. *Acta Amazonica* 30: 129-147.

Leite, R.G. and C.A.R.M. Araujo-Lima. 2002. Feeding of the *Brycon cephalus, Triportheus elongatus* and *Semaprochilodus insignis* (Osteichthyes, Characiformes) larvae in Solimões/Amazonas River and floodplain lakes. *Acta Amazonica* 32: 499-515.

Lowe-McConnel, R.H. 1987. *Ecological Studies in Tropical Fish Communities.* Cambridge University Press, Cambridge.

Lundberg, J.G. and A. Akama. 2005. *Brachyplatystoma capapretum:* a new species of goliath catfish from the Amazon Basin, with a reclassification of allied catfishes (Siluriformes: Pimelodidae). *Copeia* 2005: 492-516.

Lundberg, J.G., C.C. Fernandes, J.S. Albert and M. Garcia. 1996. *Magosternarchus,* a new genus with two new species of electric fishes (Gymnotiformes: Apteronotidae) from the Amazon River basin, South America. *Copeia* 1996: 657-670.

Lundberg, J.G., W.M. Lewis, J.F. Saunders and F. Mago-Leccia. 1987. A major food web component in the Orinoco River channel: Evidence from planktivorous electric fishes. *Science* 237: 81-83.

Mannheimer, S., G. Bevilacqua, E.P. Caramaschi and F.R. Scarano. 2003. Evidence for seed dispersal by the catfish *Auchenipterichthys longimanus* in an Amazonian lake. *Journal of Tropical Ecology* 19: 215-218.

Marlier, G. 1967. Ecological studies on some lakes of the Amazon valley. *Amazoniana* 1: 91-115.

Marlier, G. 1968. É tude sur les lacs de l'Amazonie Centrale. II. Le plancton. III. Les poissons du lac Redondo et leur régime alimentaire; les câines trophiques du lac Redondo; les poissons du rio Preto da Eva. INPA. *Cadernos da Amazônia* 11: 1-52.

Marrero, C. and K.O. Winemiller. 1993. Tube-snouted gymnotiform and mormyriform fishes: Convergence of a specialized foraging mode in teleosts. *Environmental Biology of Fishes* 38: 299-309.

Mendonça, F.P., W.E. Magnusson and J. Zuanon. 2005. Relationships between habitat characteristics and fish assemblages in small streams of Central Amazonia. *Copeia* 2005: 750-763.

Moreira, S.S. and J. Zuanon. 2002. Dieta de *Retroculus lapidifer* (Perciformes: Cichlidae), um peixe reofflico do rio Araguaia, Estado do Tocantins, Brasil. *Acta Amazonica* 32: 691-705.

Muller, S., L.H. Rapp Py-Daniel and J. Zuanon. 1994. *Ancistrus ranunculus,* a new species of loricariid fish (Siluriformes: Loricariidae) from the Xingú and Tocantins Rivers, Brazil. *Ichthyological Exploration of Freshwaters* 4: 289-296.

Muriel-Cunha, J. and M. de Pinna. 2005. New data on cistern catfish, *Phreatobius cisternarum,* from subterranean waters at the mouth of the Amazon River (Siluriformes, Incertae Sedis). *Papéis Avulsos de Zoologia* 45: 327-339.

Nelson, J.A., D.A. Wubah, M.E. Whitmer, E.A. Johnson and D.J. Stewart. 1999. Wood-eating catfishes of the genus *Panaque*: Gut microflora and cellulolytic enzyme activities. *Journal of Fish Biology* 54: 1069-1082.

Pazin, V, W.E. Magnusson, J. Zuanon and F.P. Mendonça. 2006. Fish assemblages in temporary ponds adjacent to "terra firme" streams in central Amazonia. *Freshwater Biology* 51: 1025-1037.

Petry, P., P.B. Bayley and D.F. Markle. 2003. Relationships between fish assemblages, macrophytes and environmental gradients in the Amazon River floodplain. *Journal of Fish Biology* 63: 547-579.

Piedade, M.T.F., P. Parolin and W.J. Junk. 2003. Estratégias de dispersão, produção de frutos e extrativismo da palmeira *Astrocaryum jauari* Mart. nos igapós do Rio Negro: implicações para a ictiofauna. *Ecología Aplicada* 2: 31-40.

Rapp Py-Daniel, L.H. and J. Zuanon. 2005. Description of a new species of *Parancistrus* (Siluriformes: Loricariidae) from the Rio Xingu, Brazil. *Neotropical Ichthyology* 3: 571-577.

Ribeiro, M.C.L.B. 1985. As *migrações dos jaraquis (Pisces, Prochilodontidae), no rio Negro, Amazonas, Brasil.* Unpublished M.Sc. Thesis. Instituto Nacional de Pesquisas de Amazonia, Universidate Federal do Amazonas, Manaus.

Ribeiro, J.E.L.S., M.J.G. Hopkins, A. Vicentini, C.A. Sothers, M.A.S. Costa, J.M. Brito, M.A.D. Souza, L.H.P Martins, L.G. Lohmann, P.A.C.L. Assunção, E.C. Pereira, C.F. Silva, M. Mesquita and L.C. Procópio. 1999. *Flora da Reserva Ducke: Guia de Identificação das Plantas Vasculares de uma Floresta de Terra Firme na Amazônia Central.* Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.

Sabino, J. and J. Zuanon. 1998. A stream fish assemblage in Central Amazonia: Distribution, activity patterns and feeding behavior. *Ichthyological Exploration of Freshwaters* 8: 201-210.

Sánchez-Botero, J. I. and C.A.R.M. Araújo-Lima. 2001. As macrófitas aquáticas como berçário para a ictiofauna da várzea do rio Amazonas. *Acta Amazonica* 31: 437-447.

Santos, G.M. 1982. Caracterização, hábitos alimentares e reprodutivos de quatro espécies de 'aracus' e considerações ecológicas sobre o grupo no lago Janauacá, AM (Osteichthyes, Characoidei, Anostomidae). *Acta Amazonica* 12: 713-739.

Santos, G.M. and P.S. Rosa. 1998. Alimentação de *Anostomus ternetzi* e *Synaptolaemus cingulatus,* duas espécies de peixes amazônicos com boca superior. *Revista Brasileira de Biologia* 58: 255-262.

Santos, G.M., S.S. Pinto and M. Jégu. 1997. Alimentação do pacu-cana, *Mylesinus paraschomburgkii* (Teleostei, Serrasalmidae) em rios da Amazonia brasileira. *Revista Brasileira de Biologia* 57: 311-315.

Sazima, I. 1983. Scale-eating in characoids and other fishes. *Environmental Biology of Fishes* 9: 87-101.

Sazima, I. and F.A. Machado. 1982. Hábitos e comportamento de *Roeboides prognathus,* um peixe lepidófago (Osteichthyes, Characoidei). *Boletim de Zoologia da Universidade de Sao Paulo* 7: 37-56.

Schaefer, S.A., F Provenzano, M. de Pinna and J.N. Baskin. 2005. New and noteworthy Venezuelan Glanapterygine catfishes (Siluriformes, Trichomycteridae), with discussion of their biogeography and psammophily. *American Museum Novitates* 3496: 27p.

Silva, C.P.D. 1993. Alimentação e distribuição espacial de algumas espécies de peixes do igarapé do Candirú, Amazonas, Brasil. *Acta Amazonica* 23: 271-285.

Sioli, H. 1984. *The Amazon - Limnology and Landscape Ecology of a Mighty Tropical River and its Basin.* Dr. W. Junk Publishers, The Hague.

Smith, N.J.H. 1979. A *pesca no rio Amazonas.* Conselho Nacional de Desenvolvimento Científico e Tecnológico/Instituto Nacional Pesquisas de Amazonia, Manaus.

Soares, M.G.M. 1979. Aspectos ecológicos (alimentação e reprodução) dos peixes do igarapé do Porto, Aripuanã, MT. *Acta Amazonica* 9: 325-352.

Soares, M.G.M., R.G. Almeida and W.J. Junk. 1986. The trophic status of the fish fauna in Lago Camaleão, a macrophyte dominated floodplain lake in the middle Amazon. *Amazoniana* 9: 511-526.

Turingan, R.G. 1994. Ecomorphological relationships among Caribbean tetraodontiform fishes. *Journal of Zoology (London)* 233: 493-521.

Vannote, R.L., G.W. Minshall, K.W. Cummnins, J.R. Sedell and C.E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130-137.

Waldhoff, D., U. Saint-Paul and B. Furch. 1996. Value of fruits and seeds from the foodplain forests of central Amazonia as food resource for fish. *Ecotropica* 2: 143-156.

Walker, I. 1987. The biology of streams as part of Amazonian forest ecology. *Experientia* 5: 279-287.

Walker, I. 2004. The food spectrum of the cardinal-tetra *(Paracheirodon axelrodi,* Characidae) in its natural habitat. *Acta Amazonica* 34: 69-73.

Weitzman, S.H. and R.P. Vari. 1988. Miniaturization in South American freshwater fishes: overview and discussion. *Proceedings of the Biological Society of Washington* 101: 444-465.

Winemiller, K.O. 1989. Obligate mucus-feeding in a South American trichomycterid catfish (Pisces: Ostariophysi). *Copeia* 1989: 511-514.

Zuanon, J.A.S. 1999. *História natural da ictiofauna de corredeiras do rio Xingu, na região de Altamira, Para.* Unpublished Ph.D. Dissertation. Universidade Estadual de Campinas, Campinas.

Zuanon, J. and I. Sazima. 2002. *Teleocichla centisquama,* a new species of rapids-dwelling cichlid from Xingu River, Amazonia (Perciformes, Cichlidae). *Ichthyological Exploration of Freshwaters* 4: 373-378.

Zuanon, J. and I. Sazima. 2004a. Vampire catfishes seek the aorta not the jugular: Candirus of the genus *Vandellia* (Trichomycteridae) feed on major gill arteries of host fishes. *Aqua Journal of Ichthyology and Aquatic Biology* 8: 31-36.

Zuanon, J. and I. Sazima. 2004b. Natural history of *Stauroglanis gouldingi* (Siluriformes: Trichomycteridae), a miniature sand-dwelling candiru from central Amazonian streamlets. *Ichthyological Exploration of Freshwaters* 15: 201-208.

Zuanon, J., F.A. Bockmann, and I. Sazima. 2006. A remarkable sand-dwelling fish assemblage from central Amazonia, with comments on the evolution of psammophily in South American freshwater fishes. *Neotropical Ichthyology* 4: 107-118.

Environmental Changes, Habitat Modifications and Feeding Ecology of Freshwater Fish

Norma Segatti Hahn* and Rosemara Fugi

INTRODUCTION

Environmental disturbances that expose a community to sudden changes in resource levels may elicit insights about their structuring mechanisms, such as competition for food resources or predation (Piet, 1998). Because they change the physical and chemical characteristics of water and water speed, as well as microhabitats and food sources, river impoundments are among the most significant environmental disturbances (Julio Jr. *et al.*, 1997). Human interference in natural watercourses—through the construction of dams for various purposes—has been a common practice since remote times in Brazil. For instance, the first hydropower plant was

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built on the Paraibuna River in 1889 (Petrere Jr. *et al.,* 2002). Construction of large reservoirs, especially aimed to energy generation, reached its maximum development in the 1960s and 1970s; a considerable number of large Brazilian rivers were then completely transformed into cascading dams (Tundisi, 1999). The Paraná River, for instance, the second largest drainage basin in South America, has 70% of its Brazilian portion turned into reservoirs (Agostinho et *al.,* 1994).

Change in the composition and abundance of species, with extreme proliferation of some and reduction or even elimination of others, is an unavoidable effect of impoundments on the aquatic fauna and flora (Agostinho et *al.,* 1999). The structure of the fish fauna in the first years of a river's impoundment is considered decisive in the later process of the dam's colonization, and seemingly depends on the presence of groups pre-adapted to lacustrine conditions and with great feeding and reproductive plasticity (Fernando and Holcik, 1991; Ruiz, 1998).

Most fish have enough flexibility to change their diet, i.e., when a food item becomes available, many species possess the ability to take advantage of that opportunity. The terms trophic adaptability (Gerking, 1994) and adaptive flexibility (Dill, 1983) have been used to define this behavioral plasticity—the fish's ability to change their behavior as a response to factors such as food availability, competition threats, and predation risk. This chapter will focus on the discussion of this adaptive behavior, herein termed feeding plasticity (Lowe-McConnell, 1987).

Freshwater fish in general use a vast array of feeding strategies and tactics to favor their re-adaptation to impoundment-altered environmental conditions. Trophic generalists are more favored in comparison to fish-bearing diets that are more restricted. However, some fish show rapid responses to novel environmental conditions, while others respond in a gradual manner, along years or even decades, according to their trophic nature (Agostinho et *al.,* 1999).

Considering the numerous impoundments already in operation and those on the built, studies on this research area are still scarce in Brazil. Several of those studies, emphasizing the thophic ecology of the fish fauna, were only developed after impoundment (Hahn et *al.,* 1997, 1998; Vono, 2002). However, because of the growing concern about the impacts caused by those impoundments, hydroelectric concessionaires started funding studies before the installation of dams (Gaspar da Luz, 2000; Loureiro-Crippa, 2000; Delariva, 2002; Albrecht, 2000).

Research on fish-feeding dynamics at the Upper Parana River Basin started along the construction of the Itaipu Reservoir on the Parana River (monitored from 1983-1993), and was followed by monitoring at the Segredo (1992-1995), Jordão (1995-1999), and Salto Caxias Reservoirs (1997-2001), on the Iguaçu River; in Corumbá Reservoir (1996-2000), on the Corumbá River; and at the Manso Reservoir (2000-2004), on the Manso River (Cuiabá River Basin), among others. Based on those studies and on existing literature, this chapter aims at describing alterations in food sources and use of food resources by fish after the impoundments. A case study conducted at the Jordão Reservoir is also presented and discussed. Throughout the text, the basins of reservoirs and rivers are identified only when they are other than the Upper Parana River Basin.

FOOD RESOURCE ALTERATIONS RESERVOIRS AND RESPONSES BY THE FISH FAUNA

In natural environments, the availability of food resources undergoes cyclic alterations in abundance, leading to changes in fish diets, as a result of seasonal oscillations of water temperature and level, and rainfall regime. However, these alterations are predictable and gradual and, therefore, have allowed evolutionary adjustments of the species towards an optimized use of resources under seasonally changed environmental conditions. The formation of a reservoir, on the other hand, causes unpredictable changes to which only species possessing greater plasticity (pre-adapted) can easily adapt. Some food sources available for fish suffer quick alterations, especially at the filling of reservoirs, a period characterized by intense ecological changes (Agostinho *et al.,* 1999), and during the first subsequent years.

Alterations stretch to all aquatic communities. Therefore algae, higher plants, zooplankton, zoobenthos, and fish undergo alterations in their abundances and, consequently, in their availability. In addition to changes associated with the water flow, the transformation of a terrestrial into an aquatic environment provides considerable inflow of allochthonous material during a reservoir's filling stage, especially plants and invertebrates, which become important food resources for the fish (Crippa and Hahn, 2006).

Although most fish present high feeding plasticity, which allows the exploitation of temporarily available food resources, fish with specialized food habits may encounter restrictions (a decrease in their main food source) or may be favored (an increase in their main food source) in environments that suffer sudden impacts. Changes in the availability of the most important food sources and their use by fish in the first years after the formation of reservoirs will be discussed ahead.

Terrestrial Plants

Terrestrial plants, especially fruits and seeds, have been reported as food sources for fish, particularly in tropical rivers (Goulding *et al.,* 1988; Agostinho and Zalewski, 1995; Araújo-Lima et al., 1995; Fugi, 1998; Albrecht and Caramaschi, 2003; Alvim and Peret, 2004). Some fish like the *Pterodoras granulosus,* an armored catfish of the Upper Parana River floodplain (Souza-Stevaux *et al.,* 1994), and *Auchenipterichthys longimanus,* a catfish which dwells in the lakes of the Amazon region (Amazon River Basin) (Mannheimer *et al.,* 2003), are even recognized as seed dispersers.

During the filling of a reservoir, the terrestrial vegetation is incorporated into the water as soon as the river starts flooding. In reservoirs where the riparian forest is completely incorporated into the aquatic environment, fish that depend on this allochthonous food source may be harmed in the long run, while others may enjoy this food source temporarily.

In the Itaipu Reservoir, two frugivores fish—*Piaractus mesopotamicus* and *Brycon orbignyanus*—became scarce after impoundment, and later totally disappeared from the environment. This impact was very important for commercial fisheries, given the fact that both species are large-sized and have high commercial values (Agostinho *et al.,* 1994). A reduction in frugivores species has also been recorded at the Samuel Reservoir, Amazon River Basin (Santos, 1995). On the other hand, tetragonopterine fish, such as *Astyanax* and *Psalidodon,* as well as the exotic cyprinid *Cyprinus carpio* in the Segredo and Salto Caxias Reservoirs, started showing more than 60% of terrestrial plants—especially leaves from terrestrial grasses—in the volume of their stomach contents. Actually, some tetragonopterines were among the most abundant species during the colonization period of those reservoirs.

The flooded vegetation also indirectly favors the production of other food types for fish, as soon as it starts working as substrate for periphyton colonization, for instance. Detritivore proquilodontids may use this material for a long time, provided there is enough substrate to make this resource available in the flooded environment. In the Itaipu Reservoir, decrease of *Prochilodus lineatus* population coincided with the gradual degradation of the substrate provided by the flooded terrestrial vegetation.

Aquatic Plants

Aquatic macrophytes and algae have been reported as food for some neotropical fish species (Hahn *et al.,* 1992; Andrian *et al.,* 1994; Ferreti *et al.,* 1996; Alvim and Peret, 2004). Nevertheless, unlike temperate fish fauna that encompass several herbivores species (Prejs, 1984), there are no neotropical species that use aquatic higher plants as their main food items.

The formation of reservoirs strongly influences the conditions that determine diversity and abundance of aquatic macrophytes (Agostinho *et al.,* 1999). According to Thomaz (2002), large macrophyte banks may develop on the shoreline of these ecosystems; this process can either occur soon after the reservoir is filled up, or it may take some time. No matter how long it takes for these transformations to occur and how abundant may be the aquatic plant coverage, fish rarely seem to use aquatic macrophytes as food sources in reservoirs.

In the Itaipu Reservoir, 62 species of macrophytes were recorded 15 years after its formation (Thomaz *et al.,* 1999). However, studies on the diets of 69 fish species during the first six years after the formation of the reservoir showed that only for *Pterodoras granulosus* macrophytes started being used as important food resource, comprising about 10% of the species' diet (Hahn *et al.,* 1992); after 10 years, it represented 29% of the fish's diet (Gaspar da Luz *et al.,* 2002). Similar results were recorded at the Curuá-Una Reservoir (Amazon River Basin) where, despite a great abundance of macrophytes, they were not consumed by fish (Ferreira, 1984).

On the other hand, these plants indirectly influence fish feeding, since they serve as substrate for the development of several organisms, such as periphytic algae (Esteves, 1988; Rodrigues *et al.,* 2003; Rodrigues and Bicudo, 2004; Mérona and Vigouroux, 2006) and invertebrates such as Cladocera and Copepoda, Insecta, Molluska, Oligochaeta, Rotifera, and Testacea (Junk, 1973; Bonecker and Lansac-Tôha, 1996; Lansac-Tôha *et al.,* 2003; Takeda *et al.,* 2003). At the Rosana Reservoir, the feeding habits of nine fish species associated with macrophytes were investigated by Casatti *et al.* (2003). Six species basically fed on invertebrates associated with macrophytes, and three fed on periphytic algae, but no intake of macrophytes was recorded. Macrophytes may also represent the base of herbivory and detritivory food chains (Esteves, 1988).

In contrast to macrophytes, fish consume algae (especially periphytic) in large quantities. At the Itaipu Reservoir, herbivore fish basically consumed filamentous algae in the first five years after impoundment. Of the *P. granulosus* diet, 50% consisted of the algae *Spirogyra.* Soon after the formation of the Salto Caxias Reservoir, three fish species, two detritivores *(Apareiodon vittatus* and *Hypostomus myersi)* and one omnivore *(Astyanax* sp. 'C'), began to consume chiefly filamentous algae. At the Manso Reservoir (Cuiabá River Basin) herbivores, omnivores, and detritivores fish consumed large quantities of filamentous algae in the first year after impoundment.

Terrestrial Invertebrates

In tropical environments, terrestrial invertebrates, especially adult insects, are an important food source for fish (Lowe-McConnell, 1987; Goulding *et al.,* 1988). Hymenoptera, Coleoptera, Hemiptera, Orthoptera, and Homoptera, which fall onto the water surface during flight, are among the most important insects consumed by fish (Marlier, 1967; Goulding *et al.,* 1988; Galina and Hahn, 2004; Peretti and Andrian, 2004). In a natural environment, this food source becomes available seasonally to fish; Hymenoptera, for instance, are part of the diets of the most abundant fish of the Corumbá River during spring and summer, and of two small characins studied by Bennemann (1996) at the Tibagi River, during the same period. Goulding *et al.* (1988) reported that ants are abundant in the aquatic environment during the flooding period. In flooded Amazonian forests, arboreal and terrestrial insects, especially Coleoptera, are eaten by many fish in the flooding season, particularly by the arrowanas *Osteoglossum* sp., the largest insectivore fish (circa 90 cm total length) of the Negro River.

Terrestrial environments are incorporated into the aquatic environment throughout the filling of reservoirs. Terrestrial invertebrates ordinarily not eaten by fish later become temporarily important in the diet of many species. These organisms, which after flooding become available both at the surface and the water column, are represented mainly by those more sedentary and with cryptic habits, such as earthworms (Oligochaeta) and termites (Isoptera), although Araneae, Diplopoda and winged insects are equally available and used. This highly transitory food source, however, supports for a certain period of time several fish species considered trophic opportunists. Among these fish, tetragonopterines of the genus *Astyanax,* widely distributed in South America, should be highlighted. The genus comprises small-sized fish with the ability to capture prey on the surface, especially drifting material. At the Salto Caxias Reservoir, during three years—pre-impoundment and post-impoundment phases—the diet of *Astyanax altiparanae* was based on small fruits and leaves of terrestrial plants, in addition to winged insects. However, during the time when the reservoir was being filled, which lasted three months, until the maximum water height was reached, terrestrial earthworms were extensively consumed, with a participation in the diet of approximately 40% during that specific period. During the formation and in the first year of operation of reservoirs Ponte Nova, Manso (Cuiabá River Basin), and Serra da Mesa (Tocantins River Basin), there was expressive intake of termites by anostomids of the genus *Leporinus* (Durães *et al.,* 2001; Albrecht and Caramaschi, 2003; Balassa *et al.,* 2004). Although terrestrial insects constitute a common food source for both river and stream fishes, it is believed that in reservoirs these insects are used when they are already dead and accumulated on the banks. In this case, those insects more resistant to deterioration accumulate longer on the surface, therefore being available for the fish. At the Corumbá Reservoir, *Piabina argentea* changed from a diet based on aquatic insect larvae (Trichoptera, Ephemeroptera and Chironomidae) to a diet consisting of terrestrial insects (mainly Coleoptera) in the last months of filling and in the beginning of the reservoir operation process (Ferreira *et al.,* 2002). At the Manso Reservoir (Cuibá River Basin), *Triportheus nematurus* also made use of terrestrial insects during the first year of impoundment. This species, which has an upper, surface-oriented mouth, consumed predominantly ants (Formicidae) (Galina and Hahn, 2004).

These evidences indicate that terrestrial invertebrates provide substantial contribution as an alternative fish diet resource in reservoirs, for as long as environmental conditions are unfavorable for fish to seek their regular food. This is true, however, only to opportunistic, skilled species that quickly capitalize on a very abundant food source. In this case, the mouth morphology also interferes with foraging success, i.e., fish bearing terminal and upper mouths are among the best surface explorers.

Zooplankton

Contrary to many organisms, to which the formation of a reservoir is detrimental, zooplankton has in this event an opportunity for colonization, as their population can develop quickly, soon after impoundment (Rocha *et al.,* 1999). Thus, one of the expected responses in reservoirs is an increase in zooplankton communities, as a consequence of the increase in photoautotrophic processes (Baxter, 1977). As a general trend, the first years of impoundment are characterized by high primary production resulting from the release of nutrients by the flooded organic matter, which reflects on the biological productivity increase at the other levels of the food chain (O'Brien, 1990). Microcrustaceans and rotifers were recorded as the most abundant organisms in the first three years of formation of the Corumbá (Lansac-Tôha *et al.,* 1999; Bonecker *et al.,* 2001; Velho *et al.,* 2001) and Segredo Reservoirs (Lopes *et al.,* 1997). Although rotifers prevail among zooplankton groups in reservoirs (Matsumura-Tundisi, 1999), these organisms are seldom recorded in the stomach contents of fish. Two hypotheses are usually used to explain the fact: (i) they are organisms that can be completely digested or (ii) because they are very small, they are not selected. On the other hand, microcrustaceans are the most frequently found organisms in the stomach contents of filtering fish.

The colonization of recently formed reservoirs by the zooplankton community is one of the most relevant alterations associated with food availability for fish, since this community is modestly developed in lotic environments (Margalef, 1983). However, the exploitation of this new and abundant resource will depend chiefly on the presence of fish species specialized in its consumption. At the Itaipu Reservoir, the most relevant change of fish fauna in the first years after impoundment was an immediate response to the change in zooplankton population's densities. Stocks of *Hypophthalmus edentatus,* the only fish species morphologically adapted to filter plankton (gill raker specializations), increased suddenly. Before impoundment, only three individuals had been captured, but one year after impoundment, *H. edentatus* was already the most abundant species (Benedito-Cecílio and Agostinho, 1999). It must be highlighted that its diet consisted mainly of Cladocera, a rather larger zooplankton (Lansac-Tôha *et al.,* 1991; Abujanra and Agostinho, 2002). Similar increases in zooplanktivorous fish abundance were documented at the Samuel Reservoir (Amazon River Basin) by Santos (1995), and also at the Curuá-Una Reservoir (Amazon River Basin). In the latter, two fish species that explored zooplankton *(Hemiodopsis* sp. and *Auchenipterus nuchalis)* were among the most abundant (Ferreira, 1984). A similar fact was recorded in the Salto Caxias Reservoir, although not in the same proportions as in the Itaipu Reservoir. *Odonthestes bonariensis,* introduced from Argentina and Southernmost Brazil (Bemvenuti, 1990) into this environment, also has filtering ability and feeds on Copepoda and Cladocera (Cassemiro *et al.,* 2003). After impoundment, a marked increase in the number of individuals was observed, especially during the second year, suggesting that the species behaved similarly to *H. edentatus* from the Itaipu Reservoir. At the Segredo Reservoir, where *O. bonariensis* is also captured, its diet consisted of 70% microcrustaceans, but contrary to the other reservoirs, its population increase was not significant.

On the other hand, in many reservoirs, zooplankton intake by adult fish is insignificant. At the Corumbá Reservoir, where there are no zooplanktivorous, filter-feeding species, investigation on the diets of 52 fish species during the first three years of impoundment showed that this resource occurred sporadically in the stomach contents of only a few species. In general, in reservoirs where zooplanktivorous fish do not occur, opportunistic fish use this resource as secondary or accessory food.

Even though the presence of species pre-adapted to zooplankton intake ensures the representativeness of zooplanktivore species among the most abundant fish in reservoirs, this fact does not constitute a rule. Studies conducted at the Tucuruí Reservoir (Amazon River Basin)—before and after impoundment—showed that two zooplanktivorous, filter-feeding species, *Hypophthalmus marginatus* and *Anodus elongatus,* did not become successfully established in the reservoir (Mérona *et al.,* 2001).

Zoobenthos

Benthic invertebrates, especially insect larvae (Lowe-McConnell, 1987) such as Chironomidae and Ephemeroptera, represent a valuable food source for fish in several continental aquatic environments (Goulding *et al.,* 1988; Araújo-Lima *et al.,* 1995; Hahn *et al.,* 2004). The Chironomidae are among the aquatic invertebrates most consumed by fish; this fact is associated with the high abundance of this group in many aquatic environments (Higuti and Takeda, 2002; Higuti *et al.,* 2005).

The zoobenthic community can be affected by the construction of reservoirs. According to Baxter (1977), when a river is dammed, it is expected that lotic benthos will perish and be replaced by lentic organisms. In large impoundments built in forest areas, the bottom becomes completely anoxic due to the decomposition of a large quantity of submerged plants, and a great part of the benthic resources becomes inaccessible to fish (Mérona *et al.,* 2001). Although adversely affected, the benthic community seems to quickly recolonize the new environment, especially because of the great amount of organic matter supplied by flooding, which enhances the biological yield potential (Agostinho *et al.,* 1999). O'Brien (1990) reported the importance of an early productivity of benthic invertebrates on the initial production of fish in reservoirs. Baxter (1977) pointed out that Chironomidae are well adapted to be the first colonizers in areas recently flooded by reservoirs. In fact, these organisms are among the most abundant in recently formed reservoirs (Moretto *et al.,* 2003). Higuti *et al.* (2005) documented the high abundance of this group in 30 reservoirs with different ages in the Parana River basin. The formation of the Corumbá reservoir dramatically reduced invertebrate density—especially in the reservoir's main channel—due to hypoxic conditions, while a decrease and later a recovery in organisms' density was recorded along the bank, with Chironomidae and Oligochaeta among the most abundant (A.M. Takeda, unpublished data).

The high abundance of Chironomidae in the first years of impoundment elicits many opportunistic fish species to take advantage of this resource, especially species with insectivores, invertivores, and omnivores habits, leading to increases in their populations. At the Corumbá Reservoir, 55 out of 64 species analyzed consumed aquatic insects, especially Chironomidae; for 27 species this was one of the main food items (Luz-Agostinho *et al.,* 2006). During the first year of formation of the Manso Reservoir (Cuiabá River Basin), 21 out of 24 species considered as invertivores and insectivores had Chironomidae larvae as their main food.

Macrozoobenthos is also extensively used as a food source by fish. It consists mainly of bottom-dwelling crustaceans such as shrimp and crabs that are temporarily used by fish acknowledged as piscivore (Fugi *et al.,* 2005). Usually, fish that use this resource are those also tagged bottom-feeders. These crustaceans must be more advantageous prey in terms of cost-benefit, since they are more sedentary organisms that require less investment (i.e., energy expenditure) to be captured. In reservoirs at the Iguaçu River, crabs *(Aegla* sp.) were quite abundant in the stomach contents of some fish species. In the first year of impoundment of the Segredo Reservoir, only *Pariolius* sp. was characterized as an essentially crab-feeder species, while three *Rhamdia* species plus *Crenicichla iguassuensis* fed mainly on fish, but included crabs in their diets. At the Salto Caxias Reservoir, fish initially characterized as crab feeders *(Crenicichla* sp., *Pimelodus ortmanni, Rhamdia voulezi,* and *Glanidium ribeiroi)* before impoundment became part of the piscivore fish group after that event. Although these inferences are based exclusively on stomach content analysis, it is possible that this resource disappears in an impounded environment, for the same reasons listed for smaller-sized zoobenthos. In the vicinity of the Salto Caxias Reservoir (downstream and tributaries), the above-mentioned fish continued consuming *Aegla* sp., showing that the greatest impact on those organisms occurs in the reservoir's main channel. Mollusks are another food resource consumed by fish. At the Segredo Reservoir, two specialists, mollusk-feeding species *(Astyanax gymnogenys* and *Astyanax* sp. 'G') practically disappeared from the reservoir in the first two years after impoundment, a fact that could be associated with the decrease in Molluska population in the impounded area.

Fish

In most aquatic environments, small-sized fish with great reproductive capacity and high feeding plasticity are among the most abundant, and are also a food resource available for piscivorous fish. After extensive environmental impacts, such as the formation of a reservoir, these species, especially those with short life cycle, fast growth, and high reproductive potential, will have an advantage in the colonization of the new environment (Agostinho *et al.,* 1999). That was the case with the small characins *Astyanax fasciatus, Astyanax altiparanae* and *Moenkhausia intermedia,* in the Corumbá Reservoir, and *Moenkhausia dichroura* and *Triportheus pantanensis,* in the Manso Reservoir (Cuiabá River Basin), which became more abundant after flooding. Explosions of forage species, especially fish of the genus *Astyanax,* were also observed in the Itaipu,