NATURAL HISTORY OF AMAZON FISHES

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Summary

The Amazon ichthyofauna exploits a wide variety of food types by means of an equally diverse array of feeding tactics. Food availability for fishes in the Amazon Basin is subject to strong seasonal changes, resulting in predominance of species with generalist and opportunistic feeding habits. Nevertheless, some feeding specialists such as blood-feeding candirus and scale-eating fishes do not depend on food resources derived directly from the plankton- or detritus-based food chains, or from the riparian forests. The seasonal floods in the Amazon result in an increase of the availability of shelters and peaks of food abundance for non-piscivorous fishes, which constitute the main factors controlling the reproductive activities of most fish species in large river systems. In forest streams where the floods are unpredictable and very short, local rainfall triggers the spawning activities of most fish species. During the low water period, most fishes subsist on the fat reserves they accumulated in the flooding season, but mortality by predation is intense. Such predator-prey interactions include a vast array of hunting and defensive tactics. Avoiding, hampering, or confusing predators is one of the most efficient and low cost defense alternatives, which include varied types of camouflage (in complex environments or substrates), transparency (in open water habitats), and mimicry. Nevertheless, predator-prey relations are not restricted to strictly aquatic animals, and fishes must cope with attacks of terrestrial animals as well. The obvious advances in our knowledge about the world's most diverse freshwater fish fauna notwithstanding, the Amazon region is increasingly threatened by accelerated deforestation, water pollution, advances of the agricultural frontiers, and urbanization. More information on the ecology and natural history of Amazon fishes is urgently needed before their permanent loss due to habitat destruction.

1. Introduction

Natural history is the primary source of information about organisms and their relation to the environment in which they live, leading to basic questions: What animal is this? Where does it live? How many live here? How do they survive and reproduce? Knowledge about an animal's natural history may help to formulate questions to supply and integrate different lines of biological research. In this way, natural history coupled with systematics plays an important role in recognizing and quantifying biological diversity and, consequently, helping its conservation. For instance, ecological studies depend on natural history information to make sound predictions about the effects of climate change on organisms and biological communities. Actually, natural history and behavioral studies are very reliable sources of information, and several publications stress the importance of the knowledge of animal behavior in biological conservation planning.

Ichthyofaunal studies in the Amazon began in the mid seventeenth century, when several European naturalists traveled to the region during large and long lasting (years, in some cases) field expeditions. Among these expeditions were those of Alfred Russell Wallace and of Johann Natterer, who made detailed explorations of the Negro River and its tributaries. The ichthyological collections of Wallace were lost in a shipwreck; however, Wallace survived and saved his important illustrations of fishes, which were eventually published 150 years later. The historic expedition led by the North American ichthyologist Jean Louis Rodolphe Agassiz (known as the Thayer Expedition) was also an important mark in the understanding of the complexity of the Neotropical ichthyofauna. In this initial phase, several aspects of the natural history of Amazonian fish were recorded and published as anecdotal information, almost as appendices of the taxonomic work of cataloguing species.

After this period, ichthyological studies concentrated on the understanding of a lesser number of species of commercial fishing interest, found mainly in the large, muddy, and easily reachable floodplain rivers. This biased focus on large species resulted in very scarce knowledge about the diversity, biology and ecology of the vast majority of mostly small, Amazonian fishes, as well as the details of their interactions with other species and with the environment.

Recent studies have generated valuable data that aids the understanding of the mechanisms underlying the generation and maintenance of the huge diversity of Amazonian fish fauna. However, the acquisition of information cannot cope with the accelerated rhythm of environmental and habitat degradation and losses. Hopefully the destruction process of the forest and its associated aquatic environments may be halted before irreversible losses compromise the minimal understanding of life histories of the most diverse freshwater ichthyofauna on the planet.

2. Main aquatic environments of the Amazon

The diversity of fishes in the Amazon reflects, to a large extent, the heterogeneity of available aquatic environments. Different types of aquatic environments have structural characteristics, connectivity, and dynamics that condition the presence of heterogeneous groups of species, mostly due to their biological characteristics and ecological requirements. The main types of aquatic environments available to fishes in the Amazon are

- the large floodplain rivers and their marginal floodable areas;
- the immense network of small streams that drain large portions of *terra firme* (non-floodable) forest areas;

- the rivers that drain the Guiana and Central Brazilian plateaus and that contain long stretches of rapids and waterfalls; and
- the deep channel of large rivers, characterized by great depth, absence of light, and strong currents.

Each of these environments holds a diversity of habitats and microhabitats that contribute to the existence of a large number of fish species, some of which occupy very specialized ecological niches.

In large rivers, the strong seasonal variation associated with annual flood pulses result in environments that are temporarily (but predictably) available for fishes, and harbor characteristic fish assemblages. Large sandy and/or muddy beaches harbor high species richness during the Amazonian dry season, including fishes that typically occur in these environments as well as many species of occasional occurrence. During the flooded or rainy season, the large rivers overflow their banks and spread over large areas of adjacent low-lying terrain, forming interconnected lakes and channels that sustain high biological productivity. River banks and lake edges of muddy river systems (known regionally as *várzeas*) are colonized by a diverse array of herbaceous aquatic and semi-aquatic plants, which provide shelter and foraging habitat for many fish species, including juvenile individuals of large and medium sized fish species that are the basis of commercial fisheries in the region. Extensive areas of forest are flooded for a period of several months, which coincides with the fruiting of many plant species. That is the time in which several fish species obtain a surplus of food that result in accumulation of large fat reserves allowing their survival during the dry season, when the water recedes to the large river channels. These same reserves provide the required energy for reproduction, which takes place at the onset of the next rainy season.

Most of the waters that fill the large floodplain rivers come from an immense network of small forest streams (locally known as *igarapés*), which join to form the main tributaries of the Amazon River. These small streams are not subject to the annual flood pulse, and depend on local rainfall for the maintenance of biological and ecological processes. In these forest streams, a succession of meanders causes variations in the water flow and the structure of the channel that influence the accumulation of leaf litter, sand, tree branches and trunks, tangled roots from the bank vegetation, and small rapids, each of which harbor characteristic groups of small fish species. A considerable number of these fishes occur exclusively in the small water courses, and contribute significantly to the high regional fish species richness in the Amazon. Different from large lowland rivers, small forest streams have acidic waters, are nutrient-poor and strongly shaded by the forest canopy. Their own primary production is not enough to maintain resident populations of aquatic organisms. The strong dependence upon food resources produced by the surrounding riparian forest is one of the most important ecological characteristics of Amazonian terra firme streams.

Besides composing one of the main features in the landscapes of Amazon sedimentary lowlands, the channel of large rivers harbors a very diverse ichthyofauna, composed mostly of fishes specialized for life in the darkness of those deep waters. In a broad perspective, the main channel of large rivers seems to be a relatively homogeneous environment, but this uniformity of conditions does not seem compatible with the high fish species richness found there. In fact, large river channels seem to vary in substrate composition, current speed, and depth that condition the presence of certain fish species. Recent studies resulted in the description of several new species that live exclusively in the deep channels of Amazonian rivers (e.g. the catfishes *Cetopsis oliveirai*, *Micromyzon akamai*, *Propimelodus caesius*, and *Exallodontus aguanai*). Judging from the number of unexplored rivers in the region, many more new species still await to be discovered and described from these deep waters.

The fish fauna of deep Amazonian river channels is composed mostly of catfishes (Siluriformes) and electric or knife-fishes (Gymnotiformes). The common characteristic of these groups, which probably explains their success in this environment, is the fact that they do not depend on light to move around, locate food, and find mates Catfishes usually have well developed barbels with which they recognize chemical and tactile stimuli to orient themselves and interact with other organisms. Electric fishes recognize environmental characteristics and the presence of other fishes or prey by distortions of the electric fields they generate. The absence of light in deep river channels also indicates that vision does not play an important role in the communication between these fishes, and the presence of minute eyes (in some cases even vestigial) in many of these species strengthens this hypothesis. The majority of these fish species are pale colored, often pinkish; nevertheless, the presence of contrasting dark marks in several species may indicate that they may occasionally venture into the shallow and better lit river edges. An alternative explanation is that such bold color patterns may be evolutionary retentions of morphological traits shared with related species that dwell in shallower and/or clearer waters.

Primary productivity in the deep channels, where light is almost absent, is supposed to be extremely low. Even a possible food chain based on organic detritus depends on the productivity of other parts of the aquatic environment. In this way, the predictable dependence on external food sources indicates that the majority of deep-channel fish should have a generalized diet, due to opportunistic consumption of food brought down by currents. Similarly, the absence of dark and light phases through the 24 hour cycle, associated with the unpredictable availability of food, should generate foraging patterns that do not differ greatly throughout the daily cycle. Still, it is possible that the majority of the trophic relationships among these species are based on predation, with a high proportion of carnivores and piscivores. The presence of tail portions of other Gymnotiformes in the gut of *Magosternarchus raptor*, a deep channel dwelling knife fish, seems to support this suggestion. Studies on the trophic relations between deep-channel fish assemblages are needed.

The great Amazon River, which forms the backbone of the large hydrographic basin that drains the region, is joined by a series of tributaries that drain the upper terrains of the Guianas and Central Brazil plateaus. These rivers are characterized by turbulent, fast-moving clear waters and predominantly rocky beds, and enter the Amazonian sedimentary lowlands through a series of rapids and waterfalls. In such rivers, variations in size and arrangement of rocks and in the depth of the channel create a variety of microhabitats that are occupied by an impressive number of fish species. A great part of these species depend directly or indirectly on the periphyton covering the submerged rocks as its food source. The ichthyofauna of these environments is composed of a wide variety of fish species morphologically adapted to life in turbulent waters. These fishes employ diverse feeding strategies based on grazing on algae and rock-dwelling aquatic plants (Podostemaceae), and on a diet composed of invertebrates (mainly immature insects, mollusks and crustaceans) that dwell in crevices and undersides of submerged rocks.

One of the most distinct characteristics of rapids and waterfalls is their discontinuity in the landscape. The rapids zones in the lower courses of those Amazon River tributaries are separated from each other by long stretches of deep channels, with lower water flow and (frequently) high turbidity. That set of characteristics may function as ecological barriers to the rheophilic (rapids-dwelling) fish species, resulting in the isolation of fish assemblages associated with rapids. Such isolation is supposed to have been actively splitting those fish populations over long periods (in fact, on a geologic time scale), which may have contributed to the high degree of endemism of rapids-dwelling fishes. Unfortunately, these unique environments have been strongly threatened by construction of hydroelectric dams, which changed rapids stretches into enormous artificial lakes, with environmental conditions (water flow, dissolved oxygen content, temperature, substrate, biological productivity) very different from the original situation. These environmental changes cause an irreversible loss of biodiversity (endemic species or genetic varieties) and the associated biological and evolutionary information.

Finally, it must be emphasized that the diversity of Amazonian fish fauna is not made up only by the large landscape units mentioned in this section. Special environments that frequently get unnoticed by most people (including researchers) may also hold unique species. Examples of this type of environment are underground running waters, percolating through rocky and clay-rich areas throughout the region. Both the hyporheic (waters that run in the ground under the main river beds) and phreatic waters (that fill the small interstices of the subsoil in terrestrial environments) may constitute large and unexpected environments for fishes. Recently, studies on systematics and ecology of a few small catfish species of the family Heptapteridae revealed that at least two species of the genus *Phreatobius* live predominantly in subterranean waters, appearing in wells dug as water sources in small villages. The absence of light and the very small free spaces in these environments lead to many interesting questions. How do these fish spatially orient themselves in the subterranean environment? Is there autochthonous (native, locally generated) biological productivity in these environments? What kinds of food are consumed by these catfishes? What other groups of animals live in subterranean waters? These and other questions reveal a new and exciting frontier of ichthyological and ecological research in the Amazon, and certainly more surprises are to be expected.

3. Fish diversity and community structure

The impressive diversity of Amazonian ichthyofauna (with about 3000 species) has been attributed to factors as diverse as the age and size of the drainage system; habitat succession and niche diversity made available by river, lakes, and flooded areas; the high proportion of lowlands with stable environmental conditions, capable of supporting a large abundance of fishes; and the incorporation of rivers and other basins through a diversity of geologic events, causing a mixture of fish faunas of different origins.

Table 1- Number of valid species of freshwater fishes occurring in Neotropical freshwaters and those with recorded occurrence in the Amazon. Records include Tocantins/Araguaia basin but not Magdalena and Maracaybo drainages. Main habitat refers to the habitat occupied by most species in the family. Modified from Reis et al. (2003)[a].

Family	Number of valid species	Number of species in Amazonia	Main habitat
Carcharhinidae	1	1	Marine
Pristidae	2	2	Marine
Potamotrygonidae	18	12	Freshwater
Osteoglossidae	2	2	Freshwater
Arapaimatidae	1	1	Freshwater

Megalopidae	1	1	Estuarine
Ophichthidae	1	1	Marine
Clupeidae	10	1	Marine
Engraulididae	20	11	Marine
Pristigasteridae	5	5	Freshwater
Parodontidae	23	10	Freshwater
Curimatidae	97	60	Freshwater
Prochilodontidae	21	10	Freshwater
Anostomidae	138	87	Freshwater
Chilodontidae	7	7	Freshwater
Crenuchidae	73	38	Freshwater
Hemiodontidae	28	26	Freshwater
Gasteropelecidae	9	8	Freshwater
Characidae	952	504	Freshwater
Acestrorhynchidae	15	12	Freshwater
Cynodontidae	14	11	Freshwater
Erythrinidae	15	6	Freshwater
Lebiasinidae	61	39	Freshwater
Ctenoluciidae	7	5	Freshwater
Cetopsidae	20	15	Freshwater
Aspredinidae	36	22	Freshwater
Trichomycteridae	171	56	Freshwater
Callichthyidae	177	122	Freshwater
Scoloplacidae	4	4	Freshwater
Loricariidae	673	280	Freshwater

Heptapteridae	186	94	Freshwater
Pimelodidae	83	44	Freshwater
Pseudopimelodidae	26	11	Freshwater
Ariidae	46	15	Marine
Doradidae	74	64	Freshwater
Auchenipteridae	91	68	Freshwater
Gymnotidae	19	12	Freshwater
Sternopygidae	27	17	Freshwater
Ramphichthyidae	13	10	Freshwater
Hypopomidae	25	12	Freshwater
Apteronotidae	52	31	Freshwater
Batrachoididae	5	2	Marine
Rivulidae	235	73	Freshwater
Poeciliidae	216	13	Freshwater
Anablepidae	15	2	Estuarine
Belonidae	9	6	Marine
Hemiramphidae	2	1	Estuarine
Syngnathidae	5	1	Marine
Synbranchidae	4	2	Freshwater
Sciaenidae	21	15	Marine
Polycentridae	2	2	Freshwater
Cichlidae	406	230	Freshwater
Gobiidae	40	7	Marine
Achiridae	20	6	Estuarine
Tetraodontidae	2	2	Marine

Lepidosirenidae	1	1	Freshwater
Total	4227	2100	

[a] Reis R.E.; Kullander S.O. and Ferraris Jr. C.J. (2003). Check List of the Freshwater Fishes of South and Central America, 472 pp. EDIPUCRS, Porto Alegre.

One of the most important factors of community structure of Amazonian fishes is the diversity of water types and the presence of seasonally inundated forests and grasslands. Black water rivers, such as the Negro River, have low autochthonous primary biological productivity. A study that compared fish abundance between a floodplain lake in the Solimões River drainage and another one in the Negro River showed that the former had a higher density of fish than the later. However, the number of fish species in the two lakes did not differ significantly, which means that diversity and biological productivity are independent characteristics of the Amazonian ichthyofauna.

The physical, chemical, and hydrological characteristics of lotic (running water) systems play a fundamental role in determining the distribution and dynamics of the aquatic habitats and their biological communities. These characteristics tend to vary longitudinally with the size of the streams from the headwaters to the mouth of rivers or estuaries, as well as laterally along the alluvial plains in response to seasonal inundation.

Recent studies on the ecology and distribution of gymnotiform electric fishes in the Amazon River revealed an existence of a “nodal” pattern: species richness was higher where tributaries meet the Amazon River. Yet, unlike other systems and biological groups, electric fish species richness is basically the same along the river. The contribution of the tributaries to the overall species richness is therefore local and does not cause a continuous downstream increase in electric fish species number. If the diversity pattern of the Gymnotiformes proves to apply to other animal groups or taxa, this would be an exception to the species accumulation model of community organization known for lotic communities.

In lake environments, water transparency and depth are strongly related to species richness and diversity, and may be reliable predictors of species composition. These environmental factors affect the fish assemblages both directly and indirectly. In deeper lakes with high water transparency, fish assemblages are dominated by fish predators that forage visually oriented (mainly large characins, peacock cichlids of the genus *Cichla*, and herring-like mid water predators of the pristigasterid genus *Pellona*). In shallow and turbid environments, predators oriented by tactile, chemical, or electric stimuli (mainly catfishes and the large electric eel *Electrophorus electricus*) predominate. These facts indicate that fish community structure is mediated by the predation pressure of different types of piscivorous fishes, especially during the dry season.

The aquatic communities of terra firme forest streams are not influenced by the predictable and progressive seasonal inundations, since these aquatic systems are driven by local rainfall patterns. In such streams the structure of fish assemblages depends strongly on the local physical (structural) and chemical conditions. These features have led the researchers to believe that stream fish assemblages do not change significantly over the seasonal cycle, being temporally stable. However, recent studies in the central Brazilian Amazon revealed that the composition of forest stream fish assemblages vary seasonally, with predictable changes in species abundance. Such temporal variations in the composition of the ichthyofauna indicate a general maintenance of the community structure, based on the abundance of the most common species, and higher rates of change in the occurrence of low abundance species.

During the rainy season, temporary ponds formed near to terra firme streams harbor fish assemblages influenced by factors like area, depth, vegetation cover, and the period that the pond retains water.

Fish assemblages in rapids stretches of large rivers seem to be organized by at least three main factors: food availability (mainly derived from the periphyton), shelter abundance (rocky crevices, nooks and crannies), and an apparent low predation pressure (low diversity and abundance of large fish predators). This indicates that structural complexity of the substrate in rapid areas is an important characteristic for the maintenance of a high species richness and diversity of fishes.

Besides historic and geomorphologic features, ecological factors are determinants of the composition and density of fish communities of every hydrographic system. The fish assemblages in the Amazon Basin are very dynamic, especially in the large rivers and associated floodplains, where migrations and dispersion for feeding or reproductive purposes result in composition and relative abundance changes of fish species over variable periods.

4. Time and space: activity periods, territoriality, and resource partitioning among fishes

Competition is supposed to be one of the main forces driving the evolution of the highly diverse Amazonian ichthyofauna, and it is likely that different forms and levels of resource partitioning are responsible for the maintenance of this diversity along time. One of the ways species segregate ecologically is temporal, i.e. the division of the main activity period through the daily cycle, resulting in well defined groups of diurnal and nocturnal fishes. The diurnal fish fauna is dominated by species of the Characiformes and Cichlidae, which orient themselves in their surroundings mostly visually. Such ability is employed in the formation of shoals and schools, during courtship activities, and for foraging and defensive tactics. At night, the fish fauna is composed mainly of catfishes and electric fishes that move mostly close to the bottom. As already mentioned, the low incidence (or even absence) of light in the majority of these environments lead these fishes to employ forms of orientation other than vision to perceive its surroundings, including use of chemical, tactile, sound, and electric stimuli. This temporal segregation, which has a strong phylogenetic basis in the composition of fish assemblages active during light and dark hours, results in a large number of species dividing the same space and food resources.

The knowledge about the mechanisms that support the high diversity of fish species in the Amazon region depends on analyses of spatially and temporally adequate scales. Many fish species need large areas to complete their life cycles, whereas others may do so in a few square meters of a small forest stream. The large pimelodid catfishes are renowned for the continental distances they travel to spawn. Among these, the dourada *Brachyplatystoma rousseauxii* spawns in the headwaters of the Amazon River and the larvae drift with the currents up to the confluence of the river with the Atlantic Ocean some 4000 km downstream. After staying about a year in the estuary the young douradas start migrating upriver to their spawning grounds in the headwaters of one of the turbid water tributaries of the Amazon River, a process that usually lasts for two additional years. On the other hand, some minute sand-dwelling pencil catfishes (Trichomycteridae) seem to live confined to sand banks in stream bottoms where they complete their life cycles. Dwarf cichlids and some small characin species that live associated with submerged litter banks in black water forest streams also have very small home ranges, restricted to the shallow marginal sites. Small home ranges and the sedentary (non-migratory) habits of small fish species seem to have an important role in the mechanisms that create and maintain the diversity of the Amazon ichthyofauna, as exemplified by the many species of dwarf cichlids of the genus *Apistogramma* and of the callichthyid catfishes of the genus *Corydoras.*

Cichlids are also famous by their territoriality, supposedly associated with the huge diversity of species of that family in certain tropical environments (e.g. East African Rift lakes). Nevertheless, recent data on some large species of peacock basses (*Cichla* spp.) indicate that these fishes may occupy areas of tens of square kilometers. Another group with marked territorial habits is the Loricariidae, armored catfishes with predominantly benthic habits. Loricariids build or occupy tube-like shelters in the clay banks of rivers, where they spawn and stay for relatively longs periods. No one knows if these fishes occupy the same shelters in the next spawning seasons. Other loricariid species use different types of shelters in rocky areas of river rapids, where fishes concentrate their foraging activities and spend most of their lives.

Apart from these examples of territoriality, a large proportion of the Amazonian fish species do not display this kind of behavior, or it is not maintained for long periods of time. Most of the Amazon fishes move along and among habitats following seasonal modifications of certain environmental factors, such as water temperature, dissolved oxygen, and food availability. In this roving group are included most of the species of Characiformes, a large portion of the Siluriformes, the Clupeiformes and other minor groups of fishes.

5. Reproduction: different responses to environmental factors

The peak of food abundance and the increase in the availability of shelters that result from the large seasonal floods are supposed to be the main factors that start the reproductive activities of fishes in the Amazon. The variety of reproductive strategies displayed by Amazonian fishes allow the occupation of environments where abiotic conditions and biological interactions may vary widely in space and time due to the strong seasonal flooding pulse. Different reproductive strategies are recognizable among tropical fishes, according to some attributes of their life cycles that include fecundity patterns, parental care, and population stability. There are three main species groups from the reproductive viewpoint: **equilibrium**, **opportunists**, and **seasonal strategists**.

The **equilibrium species** are mainly catfishes (Siluriformes) and perch-like fishes such as cichlids (Perciformes), but also cartilaginous fishes (stingrays, Potamotrygonidae) and the electric eels (Gymnotiformes) as well. The most important characteristics of this group of fishes are parental care of variable duration, reproductive activity weakly seasonal, and non-migratory habits. Cichlids build nests to spawn and establish territories to protect the brood, which is fiercely defended against potential predators. The duration of parental care varies between species, and is exceptionally long among pike cichlids (*Crenicichla* spp.), which may take care of young up to half of adult size. During the spawning period, male cichlids commonly display an intensified (or very different) color pattern, which probably signals to the prospective females their readiness to mate. Similarly, female cichlids change colors during reproduction, frequently displaying a brightly colored belly and boldly contrasting marks in the body and fins, such as the females of the dwarf cichlid *Apistogramma hyppolytae* (Figure 1 top left). Females of this latter species stay almost four weeks taking care of the brood, during which time they feed rarely and spend most of the time protecting the larvae and young. The attentive mothers attack fish that approach the nest, built in shallow sites, where the nestlings stay motionless, camouflaged against the substrate. Biparental care is common among cichlids. The offspring of *Aequidens* sp. are cared for by both parents that divide the tasks: the female ventilates and cleans the eggs in the nest, whereas the male takes charge of protecting the larvae within its mouth. Some species like the flag cichlids (*Mesonauta* spp.) have pelagic (open water) habits and usually lay their eggs on roots and branches of floating aquatic or semi-aquatic plants. Both parents protect the brood, patrolling the area around the nest and escorting the young while foraging amidst the floating meadows.

Figure 1a. *Attentive parents*. Cichlids are renowned for their complex and long-lasting parental care. Reproductive females of the dwarf cichlid *Apistogramma hyppolitae* adopt a boldly contrasting color pattern combined with body postures and fin flicking to send different signals (grouping, following, danger) to their brood.

Taking care of the nest, driving away intruders that approach the nestlings, or protecting the eggs and larvae within the mouth are tasks performed by one or both parents of many fish species, but few fishes supply their nestlings with food generated from its own bodies. This uncommon form of parental care is displayed by some cichlid species (*Symphysodon* spp., the popular discus fishes of the aquarium trade) that secrete a nutritious mucous substance by their skin; this substance is grazed by the larvae.

Some catfish species display other elaborate forms of parental care and protect their eggs by attaching them to their own bodies. Males of some loricariid species (e.g. *Loricariichthys* spp., *Hemiodontichthys acipenserinus*, *Reganella depressa*) carry egg masses attached to their expanded lips until hatching, whereas some aspredinids keep the eggs individually attached by stalks emerging from their belly surface.

A dweller of river and lake bottoms with large amounts of decaying organic matter, the armored catfish *Hoplosternum littorale* (Callichthyidae) spawns at the onset of the flooding season. During the reproductive period the males develop a hypertrophied pectoral spine that become curved at the tip and is employed to collect small pieces of plant debris to build a floating nest at shallow lake shores. The female helps to produce the foam that makes up the inner portion of the dome-like nest, by gulping air at the surface and expelling it below the nest. Both parents aerate the eggs and take care of the offspring.

Secondary sexual dimorphism is a common characteristic among Amazonian fishes. Temporary morphological modifications may be truly remarkable, such as those seen in the catfishes of the family Auchenipteridae, in which the males develop ossifications at the base of their maxillary barbels, and hooks and spines at the tip of a copulatory organ formed by modifications of the first anal fin rays. Some electric eels (Apteronotidae, Gymnotiformes) show such strong sexual differences that these led to taxonomic misidentifications, the male and female being described as different species. Beyond the morphological differences occasionally observable among males and females, gymnotiforms have the ability to distinguish the gender of individuals of its own species by means of the characteristics of their Electric Organ Discharge (EOD). Stronger EODs are produced by males, whereas females may display higher discharge frequencies, but this varies between the numerous species and genera of electric eels.

Stingrays in the Amazon are represented by a single family, Potamotrygonidae. These rays are ovoviviparous and have the reproductive characteristics typical of most cartilaginous fishes: low fecundity (as low as two young per litter), delayed sexual maturation, and slow growth rate. Some Amazonian stingrays show evidences of a very short parental care, which merits investigation in more detail.

The **opportunistic species** are small fishes (Cyprinodontiformes and Characiformes) that grow fast, mature early, reproduce more than once during the year and may quickly recover from population losses. Parental care is uncommon among these species, but this behavior may occur in some groups. The female splashing tetra (*Copella* spp., Lebiasinidae) jumps out of the water to lay eggs on the underside of plant leaves on stream banks. Thus, the eggs are protected from aquatic predators but are threatened by desiccation. To avoid this, the male splashes water on the eggs by means of tail beatings at the surface until the eggs hatch and the larvae fall in the water.

Seasonal reproductive activity concentrated in a single annual event is the typical strategy for many fish species in several aquatic habitats in the Amazon, and seems to be related to the effectiveness of the dispersion of eggs and larvae. Even in forest streams that are not under direct influence of the seasonal flooding pulse, there is a marked seasonality in the reproductive activities of fishes, with spawning taking place during the rainy season (which generally coincides with the overflowing of large rivers). The short duration of the floods (some hours to a few days) in the small forest streams supposedly generates a predictable increase in the availability of microhabitats and a richer supply of food for the fast-growing fish larvae. Exceptions to this general trend are the cichlids that spawn throughout the year.

The **seasonal strategists** include most of the large sized characins (Characiformes) and catfishes (Siluriformes), which show a high fecundity, absence of parental care of any kind, and that migrate for long distances to spawn in special habitats, usually the headwaters of the river systems. In general, long distance migratory species release thousands to millions of eggs (oocytes) and spermatozoids in the current where fertilization takes place. The fertilized eggs drift with the currents of the rising river waters to the floodplains, where the larvae quickly grow in the food-rich, protected environment. The very large pimelodid catfishes of the genus *Brachyplatystoma* are the prime example of this kind of strategy, migrating upstream for more than 4000 km to spawn in the headwaters of the mighty Amazon River in Peru and Colombia. For some of these species, the nursery grounds are in the Amazon River estuary, a very productive environment for the larvae. These catfish migrations are the longest seasonal fish movement in freshwater systems anywhere in the world.

Species that release gametes (oocytes and spermatozoids) in pelagic environments may show complex reproductive behavior. Long-distance migratory fishes that congregate in large schools, such as the characins *Semaprochilodus taeniurus* and *S. insignis* (Prochilodontidae), display distinct behaviors throughout their life cycles. These species are morphologically very similar and are commonly found in mixed schools during the year. During the reproductive season these fishes segregate in homospecific (one species) schools, and the peak of spawning activities take place with a temporal difference of about one month between the two species. The young-of-the-year of both species keep segregated for some time, possibly due to size difference of the individuals in the schools of each species. Nevertheless, this initial difference is quickly lessened by the fast growth rate of both species, allowing the formation of mixed schools of similar-sized fishes again. This behavioral pattern based on the asynchrony of the spawning period seems to be an example of a pre-zygotic isolation mechanism of the seasonal type, and results in a low frequency of natural hybrids during the short reproductive season.

The Osteoglossiformes are an ancient fish lineage that includes the arapaima or pirarucu (*Arapaima gigas*) and the arowana (*Osteoglossum* spp.). These fishes are large (up to 2.5 m long for *A. gigas*) and have an extended parental care displayed mainly by males. A pair of arapaimas digs a circular nest (~30 cm diameter) using the mouth and fins in shallow (~1m deep) marginal sites of lakes and backwaters, where the eggs are laid, these being guarded mostly by the male. The larvae and young congregate around the head of the parents near the surface of the water, where they can feed and breathe air. The male arowana protects its brood by guarding the eggs and larvae within its mouth most of the time initially; later the young are herded within the parent's mouth only during risky situations, such as those posed by potential predators. The parental care of the arowana lasts for about three months.

6. Feeding tactics, trophic specializations, and ecological interactions

The Amazonian fish fauna exploit a wide variety of food resources, from sessile invertebrates such as sponges and bryozoans, to insect larvae, other fish species, fruit and seeds. This wide array of food types is accompanied by an equivalent variety of morphological traits and feeding tactics. The food supply is generally subject to strong seasonal variations and is habitat-dependent, resulting in few species really specialized in some food types, and a vast majority of opportunists. Although some species may display a degree of preference for certain food types, most of them use the different food types according to their availability throughout the hydrologic cycle.

During the high water season, the flooded forests of white- and black-water rivers (called *várzea* and *igapó* forests, respectively) are stages for remarkable ecological interactions between several fish and plant species. The flooded forests are invaded by many fish species that feed heavily on fruits and seeds, building large fat reserves later used to survive during the low water season, when the waters recede and rivers return to their channels. Examples of fruit and seed eaters include the tambaqui *Colossoma macropomum*, several species of pacus and piranhas (Characidae, Serrasalminae), freshwater sardines (*Triportheus* spp., Characidae) and catfishes (mainly pimelodids, auchenipterids and doradids). However, many toothed fishes (especially characins) break the seeds during foraging, which characterize such species as seed predators. On the other hand, some large thorny catfishes of the family Doradidae (*Lithodoras dorsalis* and *Pterodoras granulosus*) ingest the seeds without destroying them, which then pass through the digestive tracts of these fishes and remain viable and germinate under adequate conditions. The seed dispersal by fish (know technically as ichthyochory) is supposed to play an important role in the maintenance of the diversity of trees in the seasonally inundated forests along the main rivers of the Amazon.

Many fish species take food from allochthonous sources (i.e. food originated from sources outside the aquatic habitat), such as insects, other invertebrates, and plant parts that fall from the nearby trees. However, some of these fishes developed adaptations that apparently increase their success of hunting terrestrial invertebrates above water. In the flooded forests of large rivers and lakes the two arowana species (*Osteoglossum bicirrhosum* and *O. ferreirai*) are the largest fishes in the world that take most of their food directly from the forest outside their aquatic habit. The capture of terrestrial animals (mainly insects and spiders, but occasionally including birds, bats, frogs, snakes and lizards) is achieved through spectacular jumps out of the water (up to 2 m high), picking prey off branches, trunks, and vines (Figure 1 top right). The ability to capture prey out of the water is partially explained by the structure of their eyes, in which the retina is divided horizontally, into superior and inferior parts, allowing a good view both below and above the water surface. Due to its acrobatic feeding behavior the arowana is also called "water monkey" by the riverine people. Dwellers of forest streams, the butterfly fishes *Carnegiella strigatta* (Figure 1 bottom right) and *C. marthae* (Gasteropelecidae) and the arowana tetra *Gnathocharax steindachneri* (Characidae) (Figure 1 bottom left) have upturned mouths and powerful pectoral fins placed high on their sides. Such morphological features allow the fish to quickly reach and catch preys as soon as they reach the water surface, and even to jump out of the water in search of prey or while evading predators.

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Figure 1b. *Sky is the limit*. The arowana *Osteoglossum bicirrhosum* is one of the most versatile predatory fishes of the Amazon. The acrobatic jumping ability of this fish allow it to reach and grab insects, spiders and other small animals perched on the riparian vegetation. Arowanas are also known to prey on fishes, birds, frogs, lizards, snakes, and bats.

Figure 1c. *Wolf in a sheep's clothes*? The characin *Gnathocharax steindachneri* joins schools of the similar looking – but small mouthed - butterfly fishes (*Carnegiella* spp.) and seems to capitalize on its morphological resemblance to make an unsuspected approach and catch water strider bugs at the water surface.

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Figure 1d. Fins or wings? The powerful pectoral fins of the freshwater butterfly fish *Carnegiella strigata* (Gasteropelecidae) are used to quickly reach and grab insects fallen on the water surface. When pursued by roaming predators these small fishes may jump out of the water repeatedly, momentarily disappearing from the predator's view.

Possibly the most important source of allochthonous food for forest fishes are insects, which are the main invertebrate prey of many species. In a broad sense, it is possible to say that almost any fish feeds on insects in at least one stage of its life. One such insectivorous fish is the chameleon characin *Ammocryptocharax elegans* (Crenuchidae), a forest stream-dweller. This fish stays motionless for long periods perched on submerged leaf blades **(**Figure 2 top left**)** or twigs, scanning its surroundings for prey with slight bending of its head and moving its eyes. After spotting a potential prey, the chameleon characin moves towards it by means of a kind of hopping over the substrate to catch the prey. Alternatively, the fish hovers shortly in the water column powered by almost imperceptible undulating movements of its dorsal fin, to grab a prey in another portion of the substrate. This behavior seems to be unique among the Neotropical characins and exemplifies how different feeding tactics may allow the coexistence of several fish species that use the same general type of food.

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Figure 2a. *Green day*. The chameleon characin *Ammocryptocharax elegans* uses its narrow and tip-curved pectoral fins to cling to the leaves' margins and fine roots, from where it visually scans its surroundings in search of minute aquatic insects. In a predominantly green surrounding the chamaeleon darter usually shows a green attire, whereas on a darker root tangle or a dead leaf, it has a drab, greyish or brownish pattern.

In the forest streams of the central Amazon, several fish species display different patterns of microhabitat use and feeding tactics linked to structural characteristics of the habitats, foraging substrates, activity periods, and morphological traits related to the acquisition of food. Along river margins and in small forest streams, the minute eleotrid *Microphilypnus amazonicus* keeps partially buried in the soft substrate with only its large and dorsally positioned eyes exposed above the sediment. Positioned this way, this fish visually finds small aquatic invertebrates on the substrate, making short and quick rushes towards the prey. Moreover, these small fishes position themselves against the current and capture tiny insects drifting downstream. But this is not the only fish that buries in the substrate to catch its prey. Some forest streams with bottom covered with white silica sand patches harbor a specialized fish assemblage that live exclusively in this kind of habitat. These assemblages of psammophilous (sand-dwelling) fishes are composed of one or more species of diurnal foragers (such as the crenuchid *Characidium* cf. *pteroides* and the trichomycterid catfish *Stauroglanis gouldingi*), and some nocturnal foragers, such as the electric knife fish *Gymnorhamphichthys rondoni* (Rhamphichthyidae) and the catfishes *Imparfinis pristos* and *Mastiglanis asopos* (Heptapteridae). Their tactics to capture aquatic invertebrates and drifting food particles vary from diurnal sit-and-wait by *C.* cf. *pteroides*, to active searching of interstitial prey buried in the sand bed by the nocturnal *G. rondoni*. A remarkable feeding tactic is displayed by the catfish *M. asopos,* which extends its long barbels and the filamentous first ray of the dorsal and pectoral fins against the water flow and uses these as a kind of net to detect drifting food (Figure 2 bottom left) grabbed with forward or sideward dashes.

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Figure 2b. *Sharing a meal*. Feeding in the rapids of clear water rivers of the Brazilian and Guiana Shields is based on the periphyton that grows attached to the submerged rocks and boulders. Two anostomids (*Leporinus maculatus* and an undescribed species of *Leporinus*) feed on the periphyton on a rock previously cleaned of detritus by the grazing activity of suckermouth catfishes (Loricariidae) in a stretch of rapids of the Xingu River in Brazil.

The origin of the food resources available for fishes along streams and rivers may change substantially. Shaded headwater forest streams depend mainly on allochthonous resources and generally harbor fish species that tend to be omnivorous generalists. However, some autochthonous primary production (i.e. generated in the aquatic system) does exist and is used by several fish species. In stream stretches exposed to direct sunlight, armored suckermouth catfishes of the genera *Rineloricaria*, *Ancistrus*, *Acestridium*, *Farlowella*, and *Parotocinclus* (Loricariidae) are the main consumers of the periphyton, grazing on the surface of submerged tree trunks, macrophytes, and rocky substrates. Grazers of periphytic algae also include some slender-bodied characin species such as *Iguanodectes variatus* and *I. geisleri.* Nevertheless, the diversity and abundance of periphytivores is usually low in small streams.

The primary productivity in floodplain rivers and lakes sustains schools of plankton-eating fish, like pelagic catfishes (*Hypophthalmus* spp., Pimelodidae) and mid water hemiodontids (*Anodus* spp. and

Hemiodus spp). An assemblage of specialized detritivores occurs further downstream and closer to river mouths, where the water flow slows down and detritus and mud accumulate. Recent studies revealed an unexpected importance of some low-trophic level fish species in the maintenance of the functioning and health of the whole aquatic system. Experiments demonstrated that the detritivore *Prochilodus mariae* (Prochilodontidae) plays a fundamental role in the transportation of particles of organic carbon (POC)—a source of energy for downstream communities. By means of its foraging activities, these fishes enhance the downstream transport and processing of organic material and ensure the proper functioning of the aquatic system and its biological community. Moreover, the absence of redundancy for this ecological function in some tropical rivers indicate that man-made alterations in fish communities, even when a single species is affected, may result in strong negative impacts for the whole aquatic environment.

Macrophytes are an important biomass in várzea lakes and along the margins of white-water rivers. Floating banks of herbaceous plants may occupy about 30% of the surface of a lake, but surprisingly few fish species feed directly from their leaves, stems, and roots. The few exceptions include the rock-bacu, *Lithodoras dorsalis*, a giant thorny doradid catfish that eats grass leaves (but also feeds on large amounts of fruits in the flooded forest), and the anostomids *Schizodon* spp. and *Rhytiodus* spp., which browse on leaves and slender macrophyte roots. Several fish species such as the ubiquitous flag cichlids of the genus *Mesonauta* use the floating macrophyte banks indirectly, as substrate for the periphyton that is grazed on. In stream habitats, mainly in slow moving backwaters, the pencilfishes (*Nannostomus* spp., Lebiasinidae) graze on algae and small associated invertebrates on submerged trees and dead trunks along the margins. These submerged trunks are also used by some armored suckermouth catfishes in a very different way: they feed directly on the wood. *Panaque nigrolineatus* and *Hypostomus cochliodon* are among the few fish species known to eat wood fragments, which are scraped with their strong spoon-shaped teeth. These catfishes apparently are able to digest cellulose with the help of symbiotic invertebrates in their guts.

Another way by which some fish consume plants directly is exemplified by rapids-dwelling fishes that dwell in the tributaries of the Amazon River. The rapids are colonized by plants of the Podostemaceae that grow firmly attached to the rocks in the most turbulent places. These plants are important food resources for some fish species like the pacus *Mylesinus* spp., *Tometes* spp., and *Ossubtus xinguense*, whose diets are composed almost entirely of these plants when adults.

Foraging in rapids implies the need to hold position in areas of high water flow speed and turbulence, which is achieved by morphologic and behavioral adaptations. Headstanders (Anostomidae) actively search for algae and sessile invertebrates by means of varied grazing tactics (Figure 2 top right). Some cichlids are also specialized for life in the rapids, such as *Teleocichla* spp. and *Retroculus* spp., and search for food particles and invertebrates using a modified sit-and-wait tactic in the turbulent waters. Loricariids feed mostly on periphytic algae and invertebrates, grazing on the rock surfaces during the night. These latter armored catfishes seem to constitute the bulk of the fish biomass in such places.

Figure 2c. *Drift net*. The sand-dwelling catfish *Mastiglanis asopos* (Heptapteridae) employs a striking and unexpected variation of the widespread sit-and-wait foraging tactic: poised on the bottom and supported by a tripod formed by its pelvic and anal fins, this fish spreads its very long barbels and the filamentous dorsal- and pectoral-fin rays, thus forming a kind of "drift-trap" used to intercept and lunge at drifting food particles.

As already mentioned, fish assemblage structure may be mediated by predation in Amazonian waters, by means of a wide array of feeding tactics. Predators may search for their prey with use of diverse strategies, from staying motionless until a prey approaches within striking distance, to chasing the prey. The energy expended in prey searching can be minimized by predators that lie in wait for their victims, camouflaged on the substrate or hiding amidst some structures that confer visual cover (plants, tree trunks). A remarkable predator that uses camouflage to catch its prey is the leaf fish *Monocirrhus polyacanthus* (Polycentridae). Living in slow flowing backwaters in streams and in the flooded forests, this fish looks like a dead leaf slowly drifting in the water column. In this way, the leaf fish approaches its unsuspecting prey (small fishes, shrimps, and aquatic insects) that are sucked with its extraordinarily large and protractile mouth, which extends up to 30% of its own body size. Trahiras (Erythrinidae) adopt a feeding tactic based on ambush, taking fish prey in a short and quick attack.

In large rivers, the biomass of lower trophic level fish species allows the maintenance of a wide variety of piscivores that use varied tactics to catch their prey. Hydrodynamic body shapes, like those exhibited by several species of piscivorous characins of the genera *Acestrorhynchus*, *Boulengerella*, *Cynodon*, and *Rhaphiodon vulpinus*, are a common morphological characteristic of predators that hunt in the upper portion of the water column and chase smaller prey fishes (see **7**). Needlefishes (*Pseudotylosurus* spp., Belonidae) also hunt for small prey fish close to the water surface in shallow margins of turbid water rivers, possibly combining a stealthy approach and short-distance darting at the prey.

In river channels, opportunistic foragers feed on small animals, plant fragments, organic detritus, and carcasses carried by the water flow. Ephemeral resources such as dead or dying animals are eagerly eaten away by piranhas (*Serrasalmus* spp.), whale catfishes (*Cetopsis coecutiens* and *C. candiru*, Cetopsidae), pencil catfishes (*Pareiodon microps*, Trichomycteridae), and some long-whiskered catfishes (mainly *Calophysus macropterus* and *Pinirampus pirinampu*, Pimelodidae). The short duration and unpredictability of these food-sources lead the fishes to eat as much as they can, and usually result in a kind of feeding frenzy around the carcass.

Some fish species specialize in feeding on living parts of other fish. Some candiru catfishes (e.g. *Vandellia* spp., Trichomycteridae) are exclusively blood-feeders when adults. They perforate branchial blood vessels of their hosts with sharp, needle-like teeth and let the victim's blood pressure gorge their straight gut. Other trichomycterids (e.g. *Pseudostegophilus nemurus*, *Henonemus punctatus*, and *Stegophilus* spp.) are specialized predators that feed on mucus and scales of other fish, scraped from their hosts by firmly attaching the mouth on the prey's body and making pendulum-like movements. Lepidophagous (scale-eating) fishes are usually found in shallow habitats and include several characin species of the genera *Roeboides*, *Roeboexodon*, *Bryconexodon*, *Exodon*, and *Catoprion*, which often have stout, external and forwards directed teeth (Figure 2 bottom right). Fin-feeding is practiced by some species of piranhas of the genus *Serrasalmus* (mostly when young). Such predatory tactics do not lead to the death of the prey, and fish species that employ them would be better qualified as mutilators. Since scales and fins of the prey fish usually regenerate after a relatively short time, it is supposed that these are renewable food sources for fin and scale-eating fishes.

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Figure 2d. Stalking ghost. The highly compressed and translucent body of the characin *Roeboides thurni* allows it to approach its unaware victims and strike on their flanks either with a widely open mouth or its mouth closed. The several outwardly directed teeth are employed to scrap off scales from the victim, which constitute the main food of this specialized predator.

Although feeding relations usually relate to predator-prey interactions, some other food-mediated, complex behavioral interactions are recorded among Amazon fishes. One such interaction is exemplified by cleaning behavior, a form or mutualistic relation where one fish (the cleaner) gets food, and the other (the client) gets rid off parasites and/or dead tissues. Juvenile individuals of the boldly patterned doradid catfish *Platydoras costatus* were recorded feeding on mucus and/or ectoparasites of a predatory fish, the trahira *Hoplias* cf. *malabaricus* in a small Amazonian stream. Such cleaning behavior seems to be rare in freshwater environments, but this may simply be a consequence of few observational studies in that kind of environment when compared to coral reefs, from where many instances of cleaning symbiosis are known. Visual contact is crucial for these complex interactions, and additional instances of cleaning behavior may be expected in clear water environments in the Amazon.

7. Predator-prey interactions: taking the chances

The often invoked image of a predator fiercely rushing towards a defenseless prey is partly unreal. Predators cannot afford to be hurt during their hunting attempts and thus they choose the most advantageous situations to secure their prey. For instance, predators quickly perceive an odd-looking or oddly-behaving individual and single it as a potential prey. These prey usually are sick, weakened, or impaired in some way (temporarily or permanently), and thus would not offer the resistance and risks posed by fully healthy individuals. However, foraging is a risky activity both for predators and prey. For instance, potential prey fish have to leave their shelters to feed, and thus are exposed to predators, which, in turn, are exposed to larger predators as soon as they initiate their predatory attempts. Thus, chances are taken both by predators and prey in such encounters.

Size alone is a risk factor for most potential prey fish: the smaller, the more vulnerable to predation. Thus, risks are lessened by the growth of the individual, which progressively increases its chances of evading predators by its increased size. However, there are exceptions to this size relationship between a predator and its potential prey. In Amazonian waters, the ogre catfish (*Asterophysus batrachus*) is able to swallow fish prey as large as about 70% its own size. This remarkable catfish has a huge gape, and a highly modified and mobile scapular apparatus. Additionally, it approaches its potential prey very unobtrusively. The small difference between the size of this predator and its prey likely prevent the latter to perceive the catfish as a threat. After frontally aiming at the head of its potential prey, the catfish opens its cavernous mouth and scoops the prey (Figure 3 top left). The catfish’s small, needle like rows of teeth prevent the prey from drawing back and thus the fleeing response makes it to advance towards the predator’s highly distensible stomach.

Figure 3a. *A cavernous mouth*. The ogre catfish *Asterophysus batrachus* (Auchenipteridae) has a huge mouth gape and takes its prey in a remarkable way: it scoops up large unaware fishes headfirst into its mouth, subsequently taking advantage of the prey's fleeing response to further its advance into its stomach.

Predators employ varied tactics to secure their prey, including stalk, ambush, attack under disguise, chase, and insinuation. These tactics relate both to the morphological and behavioral features of the predator and its potential prey, as well as to the structure and other features of the habitat the predators forage. For instance, in habitats where there is plenty of cover (vegetation, logs, rocks), predators use these to their advantage and hunt by ambush and stalk. For instance, pike cichlids (*Crenicichla* spp.) stalk with use of cover, whereas trahiras (*Erythrinus erythrinus* and *Hoplias* spp.) ambush their prey from within vegetation. In habitats with little or no cover, predators approach their prey stealthily or under disguise. Scale-eating characins (*Roeboides* spp.) often are translucent and approach their prey frontally to offer the smallest view possible to the prey. Some fin-eating piranhas of the genus *Serrasalmus* approach their victims under feint and linger close to it behaving as if not interested on the prey. When the prey becomes used to the piranha's presence and resumes its activity, the predator dash forwards and clips a fin piece of the unaware victim. Chase is a tactic often employed by predators that dwell in open habitats, where they must overcome their preys' fleeing ability. Such fishes are streamlined and able to develop considerable speed while chasing their prey, as exemplified by the 'wolf' characins, *Rhaphiodon vulpinus* and *Hydrolycus* spp. (see **6**).

The above mentioned piscivorous fishes rely mostly, if not entirely, on vision to hunt their prey, and thus their potential prey evolved features that make them inconspicuous, almost invisible. There are also many fish species that employ senses other than vision to locate their prey. For instance, freshwater stingrays are able to detect the electrical impulses generated by the muscle activity of a resting fish prey. The so called 'electric eels' (Gymnotiformes) generate weak electric discharges to locate their prey. The large electric eel *Electrophorus electricus* delivers strong electric discharges to stun its preys. Some specialized predators employ chemical, tactile, and even electric cues to locate their prey. The blood-feeding candirus (*Vandellia* spp.) apparently rely on an array of chemical, visual, and tactile cues to find their hosts. A few of these latter, in their turn, display some effective defensive tactics against these vampire fishes. The tambaqui (*Colossoma macropomum*) presses its membranous gill cover flap to prevent the slimy candiru to enter its gill chamber, employs its pectoral fin to press the candiru against its body or to flap it off, and even close both gill covers and stop ventilation entirely during an attack (Figure 3 top right).

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Figure 3b. *Vampires in the twilight*. The blood-feeding trichomycterid catfish *Vandellia cirrhosa* inhabits the murky waters of Amazonian rivers, where it lurks for its victims. Here a vampire catfish gorges itself with blood into the gill chamber of a juvenile tambaqui or giant pacu, *Colossoma macropomum* (Characidae: Serrasalminae).

Not all fish predators in Amazonian waters are other fishes; there is an array of other aquatic, as well as aerial and terrestrial vertebrate predators as well. The Amazon River dolphin (*Inia geoffrensis*) and the tucuxi (*Sotalia fluviatilis*) are versatile hunters that may herd fish and chase their prey in murky waters with use of echo-location. The giant otter (*Pteronura brasiliensis*) and the southern river otter (*Lutra longicaudis*) are skilled hunters that rely on vision and tactile sense—mostly their whiskers—to locate the prey. Other fish-eating mammals include the water opossum and the crab-eating raccoon. A remarkable fisher is the bulldog bat *Noctilio leporinus*. With use of echo-location it pinpoints fishes by the minute ripples they produce on the water surface, and grabs them with its scimitar-shaped, gaff-like claws.

Among reptiles, the most prominent fish-eaters are caimans (*Melanosuchus niger*, *Caiman crocodilus*, and *Paleosuchus trigonatus*). The two former are found mostly in rivers and lakes, whereas the latter dwells in small streams in the forest. The odd-looking matamata turtle (*Chelus fimbriatus*) is entirely aquatic, has a flattened carapace and skin flaps on the head and neck. Its camouflaging colours and its habit of staying partly buried within the leaf litter on the bottom of streams make it difficult to spot.

The matamata is an ambush predator that waits for its prey and then engulfs it with a specialized gape-suck mechanism.

However, fishes must also be aware of bird predators, which display a great variety of hunting tactics. Kingfishers usually perch above the water and wait for a fish to surface, whereas terns hover and lunge at fishes that near the water surface. The anhinga (*Anhinga anhinga*) and the Neotropical cormorant (*Phalacrocorax brasilianus*) dive to catch their prey but swallow them on the surface. Some heron species wade through the shallows and lunge at any potential prey, whereas others stir up the bottom to attract small fishes, and still others remain motionless waiting for the prey to approach. The sighting of a heron may inhibit completely the foraging behavior of small fish species such as the tetra *Hyphessobrycon eques*. In an experimental study, the tetra risked foraging in the open only when the food was highly nutritional. Thus, most Amazonian fishes must cope with both aquatic and aerial predators—a difficult task. However, the foureyes (*Anableps anableps*) has the pupil divided in two parts (Figure 3 bottom left) and thus its retina receives both underwater and aerial views of its surroundings, making it difficult to take by surprise.

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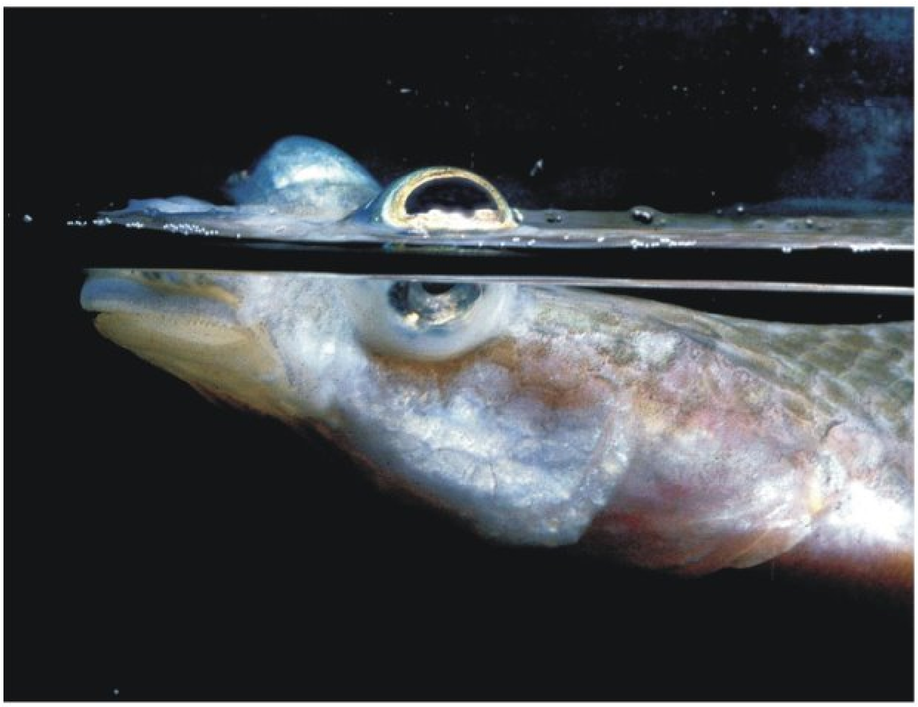

Figure 3c. *An eye on the cat and another on the fish.* The foureyes *Anableps anableps* (Anablepidae) swims at the water surface near river margins, scanning its surroundings in search of prey (mainly drifting invertebrates). Its divided eyes allow this remarkable fish to see both above and below water simultaneously, which enables it to feed while keeping an eye on aquatic and aerial predators.

8. Defense by disguise: dealing with risks posed by visually guided predators

When it comes to predators, people are used to think mostly about the visually guided ones, since humans scan their surroundings mostly with their eyes. The most widespread mode to avoid or minimize detection by visually hunting predators is camouflage or crypsis, probably due to its low energetic cost plus its efficacy against such predators. However, since movement invalidates the camouflaging effect, fishes that rely on crypsis must cope with the compromise between staying still (and protected) and feed, mate, and perform other vital activities (and be exposed to predation). Blending with the background may be accomplished by color and resemblance to the immediate surroundings, or by a disruptive pattern that obliterate the form of the animal. Several diurnal armored sucker-mouthed catfishes move inconspicuously while feeding. The long and flattened loricariines are brownish, grayish, or yellowish, with darker bars, blotches, or stripes (in addition, they adjust their color intensity to match the surroundings). The bars obliterate their contours in an example of disruptive color pattern (Figure 3 bottom right). Since several, if not most, visually guided predators rely on search images that incorporate the body contour and colors of an already known prey, disruptive patterns usually function unless the predator forms an image of camouflaged prey it found by persistent search or by chance.

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Figure 3d. *Plain as sand.* Many fishes stay exposed on the river bottom while resting, which may put them in risk of being eaten by predators. A simple but effective way of avoiding being preyed is to keep unnoticed to visually hunting predators by means of camouflage, as shown by the suckermouth catfish *Rineloricaria* sp. (Loricariidae).

Several Amazonian fish species rely on crypsis either while active or at rest. This is particularly evident for fishes dwelling in streams and shallow lakes with clear water. Blending with the substrate is exemplified by the eleotrid *Microphilypnus amazonicus* (Figure 4 top left), which dwells on the leaf litter accumulated on sandy bottoms. Resemblance to a dead leaf is another tactic Amazonian fishes rely upon. Leaves are continuously falling into the water and thus always provide an adequate background. Resemblance to dead leaves is found among unrelated, mostly nocturnal species such as catfishes and knife fishes, which rest during the day among the leaves that accumulate on the bottom or are trapped by submerged root tangles, branches, and logs. Catfishes of the genus *Tetranematichthys* exemplify such “dead-leaf” fishes (Figure 4 top right). When its diurnal shelter is disturbed, the catfish *Helogenes marmoratus* moves upwards and exposes its fore body above the water surface. Resemblance to dead leaves and escape out of the water are probably effective against diurnal, visually guided predatory fishes.

Figure 4a. *Small and unobtrusive*. The minute eleotrid fish *Microphylipnus amazonicus* dwells in shallow marginal areas of streams and rivers, where its camouflaging color pattern matches its surroundings and seems to constitute an effective defense against visually oriented predators.

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Figure 4b. *Death feigning*? The leaf catfish *Tetranematichthys wallacei* (Auchenipteridae) may stay motionless among dead leaves at the bottom of streams and rivers during the day, possibly to avoid being spotted by a predator. When disturbed at night the catfish may dive quickly into the litter accumulated on banks.

A particular instance of camouflaging against an uncommon background is provided by the chameleon South American darter (*Ammocryptocharax elegans*). This small fish dwells among the submerged leaves of the aquatic macrophyte *Thurnia sphaerocephala*, which it grabs with its modified pectoral fins. This aquatic chameleon is bright green, a feature that renders it almost invisible among the sun-bathed and continuously moving leaf blades. The fish moves surreptitiously on and among the leaves, foraging for small arthropods. Moreover, it is able to quickly change its color while moving from green leaves to dead, brownish branches or leaves.

Translucency or transparency is another defensive mode employed by a few Amazonian fishes, besides being a common feature of the larvae of most species. This defense type is found in small fish species that dwell in the water column, where no cover is available. One example is the characin *Priocharax ariel* (Figure 4 bottom left), which forages for tiny organisms in the shallows where sun rays penetrate the forest canopy and create a dance of light and shadow in the water. Several species of small, transparent shrimps are found in the same habitat, and probably add to this defense type when they rise from the bottom and swim together with the fish.

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Figure 4c. *Boldly in the open.* The small and translucent characin *Priocharax ariel* hovers at mid water near the shore of Amazonian lakes and streams, where it joins groups of similarly sized, almost transparent shrimps. The morphological and behavioral similarity with the harder-to-catch shrimps may render some protection to this small (and supposedly defenseless) fish.

Possibly the most complex defense mode related to visually guided predators is mimicry. A mimicry type rarely cited but nevertheless common among Amazonian fishes is called social or numerical mimicry. It may be conveniently illustrated by the association of two or more species of small characins that are similar in color and form, and which have no evident defenses such as venom or spines. By increasing their numbers, individuals in a group of similarly-looking fishes lessen their chances to be preyed upon based on the lesser probability to be singled out by a potential predator.

Examples of the classical Batesian mimicry among Amazonian fishes are difficult to prove and remain a controversial issue. In this mimicry type a harmless species is similar in form and behavior to a harmful one (venomous, armed with spines). The underlying argument for the effectiveness of such similarity is that predators would avoid a harmless species (the mimic) either by innate avoidance mechanisms or previous unpleasant experiences with a harmful species (the model). One putative example is the association of small tetras (*Serrapinus* and *Odontostilbe*) with the armored catfishes of the genus *Corydoras*. The latter have bony plates over the body and are armed with spines on dorsal and pectoral fins. The similarity between the tetras and the catfishes is strengthened by the pelagic habits of the latter, an unusual behavior among armored catfishes, which are habitually bottom-dwelling. An additional example, but also a controversial one, is the association of juvenile pacus (*Colossoma* spp.) with red-bellied piranhas (*Pygocentrus nattereri*), in which the former would be the harmless mimics of the latter harmful models. Another classical type, the Müllerian mimicry, is still more controversial than the precedent one among Amazonian fishes. However, it seems that the association between the small *Brachyrhamdia* catfishes and the armored *Corydoras* catfishes may be one such example, as both are armed with spines on dorsal and pectoral fins. A natural history approach, such as that used in studies on aggressive and protective mimicry in marine fishes in Brazil may be advantageously applied to Amazonian fishes as well.

Albeit not actually a disguise, but nevertheless related to avoiding visually guided predators is to remain out of sight. Several unrelated fish species, either diurnal or nocturnal, shelter within hollows in the bank or in submersed logs. Catfishes rely on this type of shelter, and some species anchor themselves with the use of erected dorsal and pectoral spines. Another shelter type is composed of soft bottoms such as mud and sand. Sandy bottoms are often found in Amazonian streams and harbor specialized sand-dwelling fish assemblages composed mostly of catfishes. One such assemblage contains the ghost pencil catfish (*Stauroglanis gouldingi*), two small and closely related catfishes (*Mastiglanis asopos* and *Imparfinis pristos*) and a knife fish (*Gymnorhamphichthys rondoni*) (Figure 4 bottom right), all of which hide in the sand when disturbed. The former is a diurnal species, whereas the remainders are mostly if not exclusively nocturnal. The pencil catfish literally dives into the sand; the two catfishes sway the body—a behavior that quickly cover them with sand—and the knife fish dives in the sand head-first.

Figure 4d. *Sand diver*. The sand knife fish *Gymnorhamphichthys rondoni* (Rhamphichthyidae) keeps buried in sand patches at the bottom of streams and rivers during the day. It emerges at dawn and spends most of the night foraging for minute aquatic invertebrates, which are caught from within the substrate with its tubular snout.

9. Conclusions and perspectives

One of the most urgent issues concerning the Amazon region is the need for strategies of biological conservation capable to assure the maintenance of the high species diversity and the ecological processes that sustain it. In this sense, the huge dimensions of the region, the different landscapes and vegetation types, the variety of aquatic habitats and the occurrence of many cases of endemism clearly indicate the need to create and to maintain a great network of protected areas.

Besides the obvious strategy of establishing a system of protected areas, it is imperative to carefully evaluate the cost-benefit relationships of man-made enterprises that potentially generate large, severe, and wide-ranging environmental impacts. Hydroelectric power plants, gold mining, deforestation for large scale agricultural purposes, and logging, forest fragmentation in rural and urban areas and water pollution, are some of the main threats to the integrity of the Amazonian ichthyofauna and whole aquatic systems. Moreover, the degree and severity of the risk to many fish species frequently cannot be evaluated simply due to complete absence of reliable data about those species.

Natural history studies are a powerful tool for conservation of the Amazon fish fauna, generating the necessary knowledge for maintenance or recovery of aquatic ecosystems and subsidizing policies of environmental control. Information derived from natural history and behavioral studies also serve as low-cost sustainability indicators for ecotourism activities. Such studies also alert for threats to the integrity of aquatic systems and its biodiversity.

Finally, it is necessary to develop a much more intense research effort than that presently underway, in order to know even the simplest aspects of life history of the fishes that dwell in the multitude of rivers, lakes, and streams of the Amazon. If this effort fails or is not made in due time, in the near future we may be left with the only—and sad—possibility of studying fishes exclusively from jars full of dead specimens in museum shelves. And even if some less demanding people may consider that option as something acceptable, we will throw away a priceless amount of information on the evolutionary history of the world's most spectacular freshwater ichthyofauna, and lose forever all the beauty and intricacy of the natural history of fishes of the Amazon.

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Glossary

Camouflage or crypsis: adaptations some animals use as protection from predators. An animal that uses camouflage looks like things in its environment. It might look like a leaf, a twig, or a rock.

Cleaning behavior: is defined as an interspecific cooperative interaction, in which a micro-carnivore (cleaner) forage on the body of other fishes (clients), the latter thus getting rid of ectoparasites and diseased tissue, and receives tactile stimulation.

Ichthyofauna: a group of fishes living and interacting with one another in a specific region under relatively similar environmental conditions.

Litter: an accumulation of dead plant remains on the soil surface.

Lotic: applied to a freshwater habitat characterized by running water (e.g. rivers, streams).

Mimicry: animals that use mimicry use colors and markings to look like another animal.

Neotropical: the region which includes South and Central America, including southern Mexico, the West Indies, and the Galapagos Islands.

Ovovivipary: the method of reproduction in which young develop from eggs retained within the mother's body but separated from it by the egg membranes. The eggs contain considerable yolk, which provides nourishment for the developing embryo.

Periphyton: organisms attached to or clinging to the stems and leaves of plants or others objects projecting above the bottom sediments of freshwaters ecosystems.

Phylogenetic: the name within biology that reconstructs evolutionary history and studies the patterns of relationships among organisms.

Prezygotic isolation: a type of reproductive isolation that occurs before the formation of a zygote can take place or prevent the fertilization of the egg if the species attempt to mate.

Systematics: the study of the diversity of life on planet Earth, both past and present, and the relationships among living things through time. Systematics, in other words, is used to understand the evolutionary history of life on Earth.

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