NATURAL HISTORY OF AMAZON FISHES

Lucelia Nobre Carvalho
Núcleo de Estudos da Biodiversidade da Amazônia Mato-grossense – Instituto de Ciências Naturais, Humanas e Sociais (ICNHS), Universidade Federal de Mato Grosso (UFMT), Brazil

Jansen Zuanon
Coordenacao de Pesquisas em Biologia Aquatica, Instituto Nacional de Pesquisas da Amazônia, Brazil

Ivan Sazima
Departamento de Zoologia and Museu de Historia Natural, Universidade Estadual de Campinas, Brazil

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Contents

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.

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Biographical Sketches

Lucélia Nobre Carvalho graduated in Biological Sciences at the Universidade Federal de Uberlândia, where she studied fish behavior by means of experimental manipulations. She obtained her MSc degree at Universidade Federal de Mato Grosso do Sul, investigating the ecological interactions of piranhas and their ectoparasites in the Pantanal wetlands of Brazil. She is PhD at the Instituto Nacional de Pesquisas da Amazônia (INPA), focusing your work on the ecology and natural history of stream fishes. She has published articles on national and international journals and her main interests include animal behavior, natural history and community ecology of Neotropical fishes.

Jansen Zuanon graduated in Biological Sciences at the Universidade Estadual de São Paulo, obtained his MSc degree at Instituto Nacional de Pesquisas da Amazônia (INPA), and his DrSc degree at Universidade Estadual de Campinas. Since 1986 he has worked as a researcher at INPA, where he acts as advisor of MSc and DrSc students. His main interests include natural history, ecology and taxonomy of freshwater fishes, and he has published scientific papers, books and popular articles on those subjects. Currently he is developing research projects dealing with ecology and conservation of Amazonian aquatic environments and their fish fauna, mainly focusing on natural history of forest stream fishes.

Ivan Sazima graduated in Biological Sciences at the Universidade de São Paulo, where he also obtained his MSc and DrSc degrees. He presently teaches Vertebrate Zoology and Vertebrate Natural History at undergraduate and graduate levels at the Universidade Estadual de Campinas, where he also acts as students' advisor at MSc and doctorate levels. His research interests span from fishes to mammals, and he has published articles on natural history, behaviour, ecology, and systematics of vertebrates in Brazilian and foreign scientific and popular journals.