AN ABSTRACT OF THE THESIS OF

Paulo Petry for the degree of Doctor of Philosophy in Fisheries Science presented on May 25, 2000. Title: Fish Assemblage Organization in the Amazon River Floodplain: Species Richness, Spatial Distribution and Recruitment Processes.

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Abstract Approved:_____

Douglas F. Markle

The composition and distribution of fish assemblages was examined in a floodplain lake system in the Amazon basin. Quantitative samples were collected during the 1992-1993 flooding season at Marchantaria Island, Solimões River. A total of 25,819 specimens representing 8 orders, 30 families, 101 genera and 139 species of fish were collected. Analysis of species richness distribution among 7 vegetation strata showed that vegetated sites had higher species richness than unvegetated sites. Stands of *Paspalum repens* had the most diverse fish fauna. Canonical correspondence analysis (CCA) was used to investigate relationship between fish assemblages and 16 environmental variables. CCA revealed that dissolved oxygen, water transparency, water depth and aquatic vegetation structure were significantly related to fish assemblage organization. The results suggest that physiological adaptations to hypoxia and habitat complexity play a major role in the organization of these assemblages. The morphology, ontogenetic development, shape variability and deposition of otolith microincrements are described for floodplain serrasalmin fishes. Serrasalmin otoliths were similar to other ostariophysan, nevertheless their shape was species-specific. Elliptical Fourier analysis showed that *Mylossoma*

aureum lapilli were highly variable in shape when compared to closely related species. PCA and discriminant function analysis indicated that two distinct forms of lapillus can be recognized for *M. aureum*, and intra-species variation was higher than inter-species variation. Otolith microincrement analysis was tested for these fishes, and microincrement deposition validation showed that *Piaractus brachipomus* deposits otolith increments on a daily basis. Patterns of spatial distribution, growth and mortality characteristics of larvae and juvenile were examined for *M. aureum* inhabiting the Marchantaria Island floodplain. Otolith-derived birth date reconstruction showed that *M.aureum* spawning season extended from late November to March, and peak larvae recruitment to the island occurred in mid-December. Larvae and juveniles had different spatial distributions in relation to habitat usage. Instantaneous growth coefficients (g) varied from $0.0197(d^{-1})$ to $0.265(d^{-1})$ among cohorts. Early-season cohorts had wider otolith microincrements and higher instantaneous growth coefficients than late-season cohorts. Mortality estimated by the decline of $\log_e$ (abundance) regressed on age indicated that cohort-specific instantaneous mortality varied significantly among cohorts, ranging from $0.027(d^{-1})$ (2.6%/d) to $0.103(d^{-1})$ (9.7%/d).

Fish Assemblage Organization in the Amazon River Floodplain: Species
Richness, Spatial Distribution and Recruitment Processes

by

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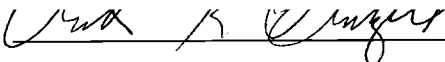Commencement June 2001

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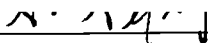
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CONTRIBUTION OF AUTHORS

Dr. D. F. Markle was involved in the sampling design, data analysis and writing of each chapter. Dr. P. B. Bayley contributed with original unpublished data for chapter 2 and was involved in revising the statistical analysis of chapters 2 and 4. Field data collection and processing were done with the assistance of field technicians from National Institute of Amazon Research (INPA) in Manaus AM, Brazil.

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José Fernandes (Curari) *in memoriam*

Fish Assemblage Organization in the Amazon River Floodplain: Species Richness, Spatial Distribution and Recruitment Processes

Introduction

The objectives of this thesis were to understand the dynamics of young fish assemblages that use the Amazon River floodplain as their nursery habitat. I investigated the relationship among species diversity, fish assemblages and recruitment processes influenced by environmental conditions in the Amazon river-floodplain system. I begin by describing the natural setting of the environment and how the annual flood pulse influences the system. I characterize taxonomically the fish community inhabiting the floodplain, and examine its distribution patterns in relation to habitat use and environmental gradients.

I describe and characterize the morphology, shape and microstrucutral characteristics of otoliths (inner-ear bones) and test their properties as time keeping structures that can be used to estimate age and growth in a daily basis. I validate the microstructure deposition chronology and suggest a procedure to be adopted for further use of this technique in recruitment studies of ostariophysan fishes. Subsequently I used otolith-derived age and growth estimates to analyze the recruitment patterns of the early life history stages of *Mylossoma aureum*, a commercially important food fish in the Amazon basin.

Chapter 1

The Amazon River-floodplain System, Landscape Description and Flooding Regime

The Amazon floodplain landscape

The Amazon basin is the largest freshwater system on earth, with an area of more than 6 million km^2 and is responsible for 1/5 of the total annual freshwater contribution to the world's oceans. The Amazon River originates in the Andes and flows 6500 km eastward, crossing the Sub-andean Trough and the Central Amazonian Plain to reach the Atlantic Ocean. With an annual average discharge of about $5.5*10^{12}$ m^3/year (Sioli, 1984), the Amazon carries a considerable load of sediments consisting of fine sand and clays (on the order of 1.1 billion tons/year) mostly of Andean Origin, (Gibbs, 1967). These sediments are gradually deposited as the river flows through the basin (Mertes, 1985). After leaving the Andes, the Amazon altitudinal gradient is significantly reduced. While crossing the Central Plain between Iquitos and Manaus (2100 km) the declivity is 4cm/km, and from Manaus to the ocean (1500 Km) the gradient is reduced to only 1 cm/km.

The landscape of the central plain lowlands, from Iquitos, Peru to the ocean, is dominated by a vast typical fringing floodplain (Welcomme, 1979). The floodplain (hereafter referred to as *varzea*) may be as wide as 50 km in

the upper reaches and up to 100 km in the lower reaches and is surrounded

by Tertiary and Quaternary terraces. Soils in the varzea are characterized by

horizons of alternating coarse and fine sediments (Irion et al., 1983). The

deposits are due to combination of sedimentation from the main channel, side

channels and over bank flow (Mertes, 1985), as well as wide annual water

level fluctuations (Irion et al., 1983). The geomorphology of the varzea is the

result of the sum of the hydraulic characteristics of the river; slope, channel

attributes (width and depth), sedimentation patterns, structure, and the recent

geologic history.

Sedimentation and erosional processes are among the most important

processes through which the Amazon varzea landscape is modified. These

processes have resulted in the development of a geometrically complex

floodplain, giving the channel an anastomizing pattern (Mertes, 1990). The

floodplain is a complex system of islands, side channels, levees, channel bars

and floodplain lakes, which results in a mosaic of geomorphic structures and

biotopes. Side channels, locally called "*paranas*", flow between islands and

often flow several kilometers into the floodplain, providing a pathway for

transport of sediment on and off the floodplain (Mertes, 1985).

Bayley and Petrere Jr, (1989) presented an integrated estimate of

floodplain area for the Amazon basin, their results suggest that flooding takes

place over an area of 180,360 km^2. Sippel et al., (1992) estimated the area

of the varzea, along the Amazon main stem between the Peru-Brazil border

and the Atlantic, at approximately 94,000 km^2, showing that the floodplain of

the Amazon main channel represents half of the total area influenced by the

flooding in the entire basin. Mertes (1990) suggests that 1/6 of the varzea is

not inundated on a regular basis by the river, whereas 2/3 is regularly

inundated and the remaining area is covered by permanent floodplain lakes.

Floodplain lakes are a keystone element in the dynamics of biological

production within the floodplain. The active lateral exchange of water

between the main channel and lakes rapidly recycles sediments, nutrients and

organic matter (Junk et al., 1989). Most of the primary productivity derived

from the varzea is concentrated in the floodplain lakes, where vast aquatic

grasslands develop along the shorelines. Some of the C_4 plants may produce

up to 100t/ha/yr of biomass (Piedade, 1993). Sippel et al., (1992) estimated a

total of 6510 floodplain lakes along the 2800 km of the Brazilian Amazon main

stem that cover an area of 10370 km^2, representing 11% of the varzea.

Although only 10% of the lakes are larger than 2 km^2, they compromise more

than half of the total lake area. The largest lakes have an area of more than

60,000 ha, while the smallest vary between 1 and 2 ha at low water stages.

Floodplain lakes can be classified into two groups according to their

hydrology: those with their own drainage and local runoffs and those without a

local drainage normally found on islands. Floodplain lakes with their own

drainage account for 92% of the total number of lakes in the varzea (Sippel et

al., 1992), and are distributed on either side of the river. The dominant

component of the annual water budget in many of these lakes is local rainfall

runoff, and main stem inflow only accounts for 1/5 of the total water input to

the lakes (Lesack and Melack, 1995). Island lakes account for the remaining 8%, and their hydrology depends mainly on river input. Many of these lakes become totally isolated from the river during low water period, and those with permanent connections drain into the river during declining and low water levels (Forsberg et al., 1988).

The flood pulse in Central Amazonia

Circumtropical regions usually have pronounced alternation between a dry and a rainy season. In the Amazon because of the seasonal shift of the intertropical convergence zone, the maximum rainfall in the southern part of the basin usually occurs two months earlier (Dec.-Feb.) than in the central part of the basin, and six months earlier than (Jun.- Aug.) the northern part of the basin (Meade et al., 1991). Precipitation within the basin is variable, ranging from less then 2,000 mm/yr in the northeastern and southeastern sides of the basin and up to 7,000 mm/yr on the east side of the Andes (Salati et al., 1979), with an overall average precipitation of 2300 mm/yr throughout the basin, (Salati and Marques, 1984). The Amazon flood wave is generated as the consequence of this highly seasonal rainfall.

Large tropical rivers such as the Amazon tend to have monotonic unimodal hydrographs, usually with large amplitude and long duration (Welcomme, 1979; Lowe-MacConnell, 1987). In general, seasonal floods in the tropics move downstream at a speed between 11 and 29 km/day

(Welcomme, 1979), and can take several months to travel along the basins.

The peak of the Amazon flood wave moves downstream at a rate of 25

km/day (Richey et al., 1989a), and takes approximately 85 days to travel

between Iquitos and Manaus. Although water level in the main stem at

Manaus fluctuates 10 m or more, the discharge only varies by a factor of 2-3

during a hydrologic cycle. This small range in discharge can be mainly

explained by the seasonal difference between peak discharge from the

northern and southern tributaries, which is a result of the offset of the rainy

season between the two sides of the basin (Meade et al., 1991), and by the

important exchange of water between floodplain and main stem. As much as

30% of the flow in the main stem is derived from or stored on the floodplain

during the flood cycle (Richey et al., 1989a). The inundation of the floodplain

is highly dependent upon local geography; the flood is not a typical over bank

flow until the river exceeds the elevation of most levees (Mertes, 1990).

Historical records from the Manaus gauge station (1904 - 1994) show

that the average hydrologic year (length in days between consecutive annual

low stages) in the central part of the basin ranges from 305 to 421 days and

has an average 364.3 days (± 24.4, n=90) (Fig. 1.1a and f). The hydrograph

is highly coupled to the El Niño Southern Oscillation (ENSO) cycle on a 2-3

year time scale, with discharges linked to atmospheric circulation changes

over the tropical Pacific Ocean (Richey et al., 1989b). Major ENSO events

reflected in low discharges, whereas high discharges were associated wit the

positive phase of the Southern oscilation. Although discharge nearly triples
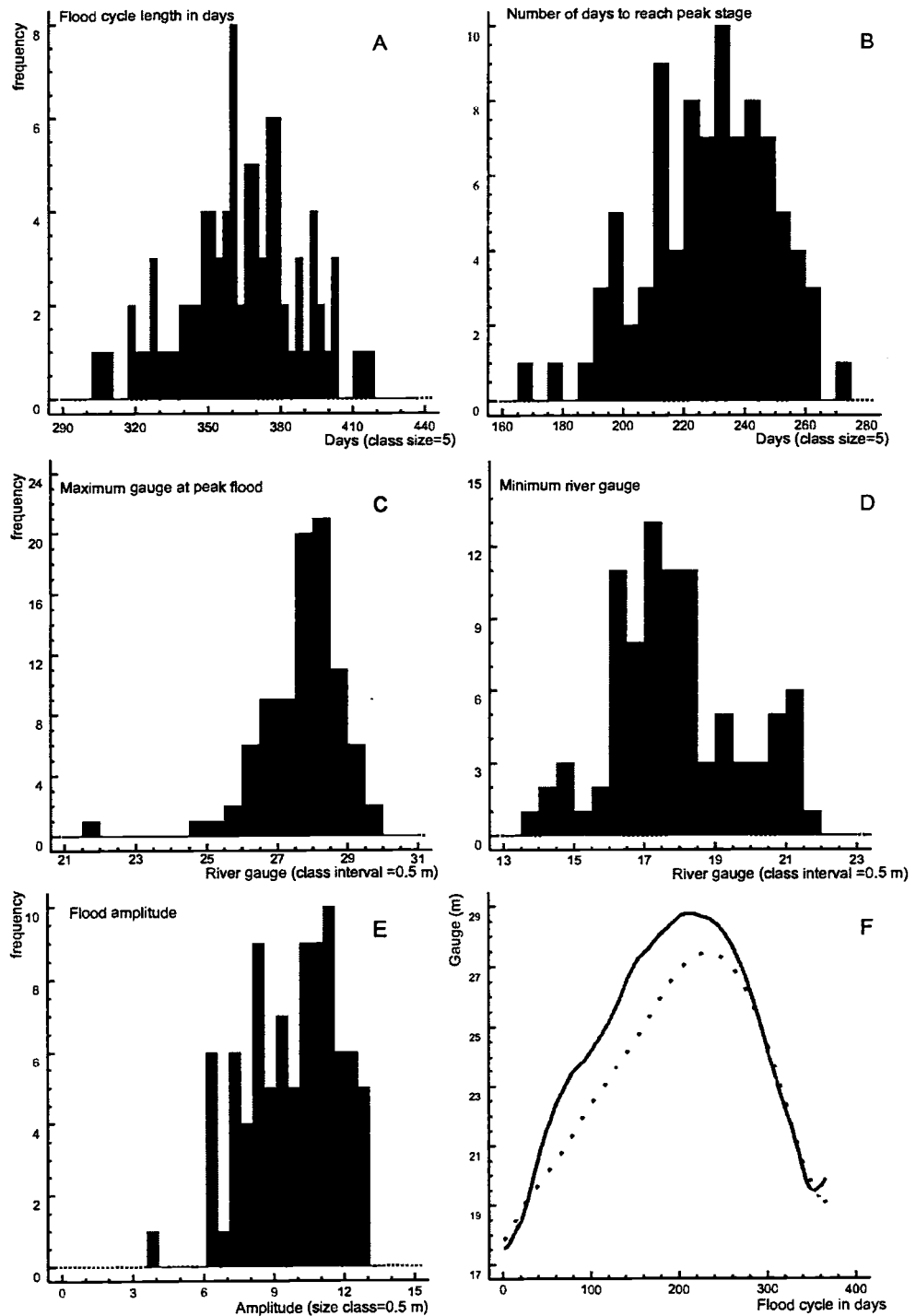
Figure 1.1. Hydrologic characteristics of the Amazon flood pulse at the Manaus harbor (1904-1994). Frequency histograms summarizing the flood pulse variability (A to E). Average flood cycle hydrograph, dotted line, and 1992 -1993 flood hydrograph, solid line (F).

from low water to peak stage, it takes more than 6 months for the water to rise. At Manaus, the average time from low stage to peak stage during a hydrologic year is 228.4 days (± 20.8, n=90), with a range of 166 to 273 days (Fig. 1.1b). The average high stage is 27.69 m (± 1.16, n=90), with a range from 21.66 to 29.69 m (Fig 1.1.c), whereas the average low stage is 17.87 m (± 1.82, n=90), with a range from 13.84 to 21.64 m (Fig. 1.1d). Flood amplitude (difference between high stage and low stage in a given flood cycle) ranges 4.1 to 13.02 m with an average of 9.83 m (± 1.97, n=90) (Fig. 1.1e). Although the flood cycle is recurrent and predictable, the rising velocity (slope of the hydrograph) and occurrence of retreats in rise (falling stages within a general trend of increasing stage), locally called *"repiquete", are* unpredictable, and dependent on the precipitation offset between the southern and northern part of the basin and local rainfall. An analysis of the hydrographs from the Manaus harbor gauge station between 1904 and 1990 revealed a total of 93 retreats. Twenty years (23.2%) within this period had no retreats, 44 years (51.1%) had 1 retreat, 17 years (19.7%) had 2 retreat, 4 years had 3 retreats and 1 had 4 retreats (Fig. 1.2a) The duration of the retreats ranged from 2 to 70 days (Fig.1.2b), with a magnitude ranging between 0.02 and 3.83 meters(Fig. 1.2c). Over 50% of the retreats had a duration between 2 and 3 weeks, with mean magnitude varying between 0.57 to 1.04 m and daily mean stage drop of 0.03 meters (table 1.1).

The accentuated seasonal variation in river level results in dramatic changes in the surrounding landscape and directly influences the dimensions

of the aquatic habitats associated with the floodplain. Lake surface area can expand six to ten times, and depth may change from less than 1 m at low water to 11-12 m at high flood.

Table 1.1. Amazon river stage retreats (*repiquetes*) registered during the rising limb of the hydrograph at the Manaus harbor gauge station between 1904 and 1990 (86 years, 93 retreats).

Time-Days	Number of retreats	Mean amplitude (m)	Mean drop/day (m)
1-7	14 (15%)	0.065	0.013
8-14	23 (24.7%)	0.138	0.013
15-21	27 (29%)	0.573	0.032
22-28	11 (11.8%)	1.04	0.042
29-35	8 (8.6%)	1.14	0.034
36-42	7 (7.5%)	1.09	0.029
43-49	1 (1%)	0.8	0.018
50-56	1 (1%)	3.83	0.073
70	1 (1%)	1.3	0.018
Mean		0.57	0.03

While water is rising, there is a sequential transformation of a terrestrial system into an aquatic system. Such a large and long flood pulse becomes the major driving force of biological interactions in the Amazon river-floodplain system (Junk et al., 1989). The entire biota associated with the floodplain has evolved in synchrony to the flood regime. There is a visible elevational gradient in which aquatic and nearly permanent terrestrial conditions oscillate. On terrains of higher elevation, which may be flooded for short periods during a typical year, but often remain dry for several years in a row, vegetation is a lush flood-tolerant forest of about 350 species of trees (Junk, 1989), and 273 species of shrubs and terrestrial herbaceous plants (Junk and Piedade, 1993).
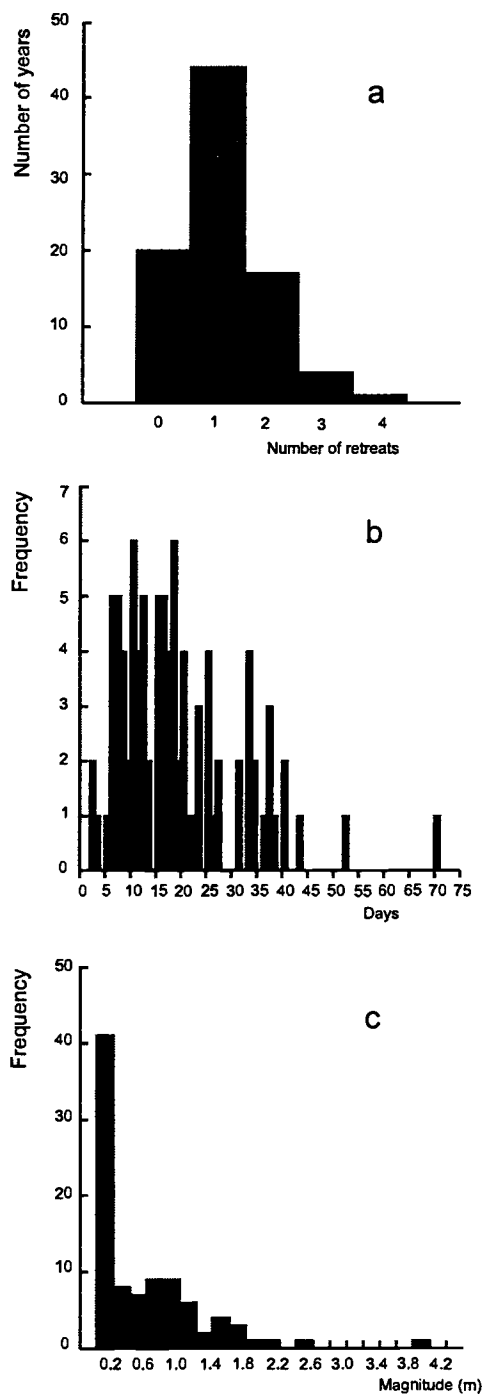
Figure 1.2. Frequency histograms of Amazon river stage retreats during the rising limb of the hydrograph, recorded at the Manaus harbor gauge station between 1904 and 1990. Number of retreats per year (a), retreat duration in days (b) and retreat magnitudes in meters (c).

On lower terrains, which might remain flooded up to 9 months, there are plants with short reproductive cycles, such as grasses and herbs. Aquatic macrophytes are an important component of the vegetation in these low-lying terrains. Junk and Piedade, 1994 recognized a total of 41 species of aquatic plants, mostly emergent , that occur on a single island, many of them with adaptations to survive a terrestrial phase. These plants occupy certain habitats according to their particular ecological requirements (Piedade et al., 1992).

Description of sampling area

Fieldwork for this study was conducted on Marchantaria Island, an island located 14 km southwest of Manaus (3E 15' 04" S and 59E58' 22" W), 200 km south of the equator and 1500 km from the mouth of the Amazon River (Fig. 1.3). It is the lowest island in the Rio Solimões, which is the name of the Amazon River above the confluence with the Rio Negro. During high flood stage (at river stage 27 m and above at the Manaus harbor), the island in 1993 was about 11 km long and 3.7 km wide at its widest stretch, (based on SAR images, 25 m pixel resolution) with the longest axis in the east-west orientation. The island has an area that varies from 33.8 to 37 km^2 depending on the river stage. Above river stage 27 m most of the island is flooded (11.3 km^2 covered by flooded forest and agricultural fields, 16.1 km^2 covered by aquatic vegetation, and 5.5 km^2 covered by open water).
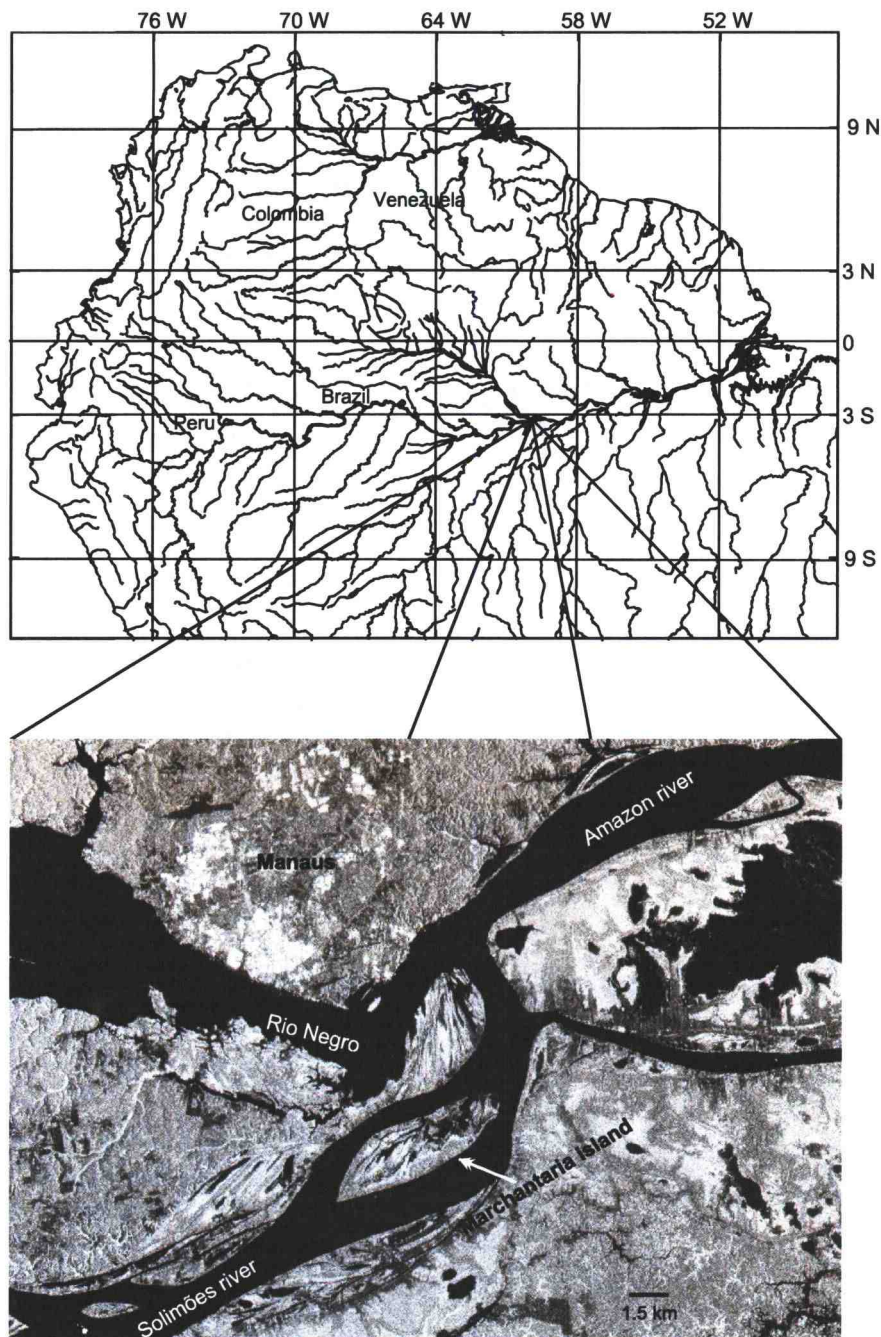
Figure 1.3. Map of the Amazon Basin showing the location of Marchantaria Island in the vicinity of Manaus. Synthetic Aperture Radar (SAR) image from JERS-1, 50 m pixel resolution, acquisition date Feb. 23. 1993, Nasda – Japanese Space Agency).

Aquatic macrophyte coverage and lake surface area vary dramatically during the flooding cycle. Marchantaria probably originated as a stable channel bar on which sand bars began to accumulate (Irion et al., 1983). Ridges 10's of meters wide extend over more than half of the island, in groups more or less parallel to each other, and parallel to the flow dominating the surface morphology of the island. The upstream side of the island is 5 to 6 meters higher than the downstream part and ridges are less pronounced. The eastern side of the island (downstream end) is a very active sedimentation zone, where large amounts of sediment are continually deposited forming sandy channel bars composed of mega-ripples with crests approximately 15 m apart and height of 70 to 80 cm (Irion et al., 1983). During the dry season, terrestrial herbaceous plants and semi aquatic plants colonize the exposed mega-ripples. The growth of monospecific stands of *Salix humboldtiana* and *Echinochloa polystachya* stabilizes the surface and provides substrate for further sediment deposition, triggering the island growth on its down-stream side. Establishment of these plants depends largely on tolerance to inundation, and the local hydrological regime. The perturbation caused by the flood pulse forces an annual setback in plant community development, maintaining the low-lying terrains at low seral stages often for decades of longer (Junk and Piedade, 1993). During flooding, terrestrial herbaceous vegetation is replaced by predominantly aquatic macrophytes. As a consequence a great variety of microhabitats become available for colonization by incoming aquatic fauna. Inside the island are several

floodplain lakes of various sizes., which are separated by higher terraces covered by a diverse lush floodplain forest, while lakeshores are covered with large patches of aquatic macrophytes. The most frequent free-floating species of macrophytes are *Eichhornia crassipes*, *Pistia stratiotes* and *Salvinia spp.* Aquatic and semi-aquatic grasses are mostly *Echinochloa polystachia*, *Paspalum repens, Paspalum fasciculatum, Panicum sp* and *Oriza perenis.* Because of the flooding regime, large floating patches of aquatic macrophytes derived from upstream lakes drift down the river and are recruited to the island's bays and lakes. *Eichhornia crassipes, Paspalum repens* and *Pistia stratiotes* may form large floating meadows that move around the lakes driven by winds. The interior of the island is dominated by monospecific stands of *Echinochloa polystachia*, which covers 5-6 km^2 (Piedade et al, 1991). This grass is rooted to the ground, forming compact stands, and the stems grow as fast as the water rises. On the edges of *Echinochloa polystachia* stands, borders of *Paspalum repens* are typically found, initially attached to the bottom through long stems, but become free floating as water depth exceeds about 4m. Such stands of *P.repens* might be several kilometers long, and about 15 to 20 m in width. Environmental conditions inside the lakes, especially along the shorelines, vary considerably during a flooding season. Water transparency may vary from 15 cm near the river, to 1 meter inside the floodplain. Because of massive production of organic matter by aquatic plants and high decomposition rates, hypoxic conditions are frequent occurrence inside the varzea. Oxygen deficiency

prompts the production of hydrogen sulphide. The duration and intensity of hypoxic conditions are largely determined by the rate of water input from the river and windstorms. Sites closer to the river with constant water renewal have higher oxygen concentration and higher sediment load, whereas sites further inside the island at the expanding edge of the flood have low water input, become more transparent, and commonly hypoxic.

The hydrology of the island closely reflects the hydrograph recorded at the Manaus harbor gauge station (Schmidt, 1973). On a regular hydrologic year, the lower terrains become flooded in early December, and maximum flooded area will usually occur in May when water level exceeds the 27 m stage. During the 6-month flood, there is a tremendous lateral and vertical expansion of the aquatic environment, which becomes the prime nursery area for larval and juvenile fishes, many of which are transported into the floodplains at the onset of the flooding cycle (Petry, 1989).

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Chapter 2

Fish Assemblages in the Amazon River Floodplain: Species Composition, Habitat Usage and Organization along Environmental Gradients

Abstract

The taxonomic composition, and the distribution of fishes were examined in a floodplain lake system in the Amazon basin. Quantitative samples were collected during the flooding season of 1992-1993 at Marchantaria Island, Solimões River. A total of 25,819 specimens representing 8 orders, 30 families, 101 genera and 139 species of fish were collected. The distribution of species richness among 7 vegetation strata was analyzed. Vegetated areas had significantly higher species richness than unvegetated area. Stand of *Paspalum repens* harbored the most diverse fish fauna. I examined the relationship between the structure of fish assemblages and 16 environmental variables. Canonical correspondence analysis revealed that dissolved oxygen; water transparency, water depth and aquatic vegetation structure were significantly related to fish assemblage organization. The results suggest that physiological adaptations to hypoxic conditions and habitat complexity play a major role in the organization of these assemblages.

Introduction

Resource availability, environmental variability and biotic interactions have been invoked as the most common mechanisms regulating the composition, abundance and distribution of species within and among biological communities (Menge and Sutherland, 1987). The relative influence of biotic and abiotic factors in structuring and regulating fish assemblages in streams and rivers has been controversial, leading to polarized views as to the stochastic versus deterministic controls of community structure (Grossman et al., 1982; Moyle and Vondracek, 1985; Schoener, 1987; Grossman et al., 1998). Abiotic conditions can modulate the composition and distribution of fish assemblages according to their physiological tolerances to environmental conditions and availability of suitable habitat. Fishes with similar requirements tend to co-occur, forming distinct assemblages (Weaver et al., 1996). Factors such as pH, oxygen concentrations, water turbidity and depth gradients have often been implicated in structuring fish assemblages (Tonn and Magnuson, 1982; Junk et al., 1983; Rahel, 1986; Brazner and Beals, 1997; Rodriguez and Lewis, 1997; Tejerina-Garro et al., 1998). Nevertheless, spatial structural habitat complexity has also been shown to be an important factor in structuring assemblages (Eadie and Keast, 1984; Benson and Magnuson, 1992).

Habitat heterogeneity is related to fish diversity in streams and in lucustrine systems (Gorman and Karr, 1978; Tonn and Magnuson, 1982;

Eadie and Keast, 1984; Benson and Magnuson, 1992; Weaver et al., 1996; Weaver et al., 1997). Aquatic macrophytes have been recognized as important promoters of habitat complexity and heterogeneity. Vegetation presence was considered the primary habitat dimension along which species packing and niche segregation is organized, thus vegetation diversity is the main factor related to species richness in aquatic systems (Tonn and Magnuson, 1982). Spatially complex habitats may incorporate a greater variety of microhabitats potentially supporting a more diverse community (Tonn and Magnuson, 1982; Eadie and Keast, 1984; Dibble et al., 1996; Weaver et al., 1997). Substrate diversity and vegetation complexity were the best predictors of fish species diversity in southern Ontario lakes (Eadie and Keast, 1984).

Although structural characteristics of macrophytes stands represent an important aspect of habitat selection by fishes, biotic interactions among fish species are mediated by the presence of macrophytes (Savino and Stein, 1982; Savino and Stein, 1989; Heck and Crowder, 1991), thus fish distribution and abundance in relation to the presence of macrophytes may not be simple (Weaver et al 1996). Several studies have shown that in response to the presence of piscivorous predator, fish shift their microhabitat distribution and seek shelter (Werner et al., 1977; Goodyear, 1973; Seghers, 1974; Stein, 1979). Roots, leaves and stems provide efficient visual and swimming barriers and mediate the extent by which predators interact with prey (Savino and Stein, 1982). Predation rates decline as habitat structural complexity

increases (Crowder and Cooper, 1979; Savino and Stein, 1989). Tonn et al., (1992) showed that offshore pelagic habitat was underutilized by prey species because of the presence of predators. Similar findings were reported by Winemiller, (1989) for the inhibitory effect of piranhas (*Pygocentrus sp*) on the distribution of other species in the Orinoco basin and by Jackson, (1961) for the African tigerfish (*Hydrocynus sp*).

The Amazon basin contains a complex river-floodplain system, with seasonally variable numbers of floodplain lakes that are subjected to a cyclical flood pulse. This annual pulse produces and maintains highly diverse and dynamic habitats (Junk et al., 1989). The diverse community of aquatic macrophytes and flooded forest in the floodplain constitutes the most important element in determining the structure, diversity and heterogeneity of aquatic habitats. Abiotic factors such as oxygen concentrations were reported as important limiting factors determining the spatial and temporal variation in fish assemblages (Junk et al., 1983). Although strong associations between fishes and macrophytes were reported for several areas in the Amazon (Bayley, 1983; Junk et al., 1983; Araujo-Lima et al., 1986; Henderson and Hamilton, 1995; Henderson and Robertson, 1999) and Orinoco (Machado-Allison, 1990), the relationship between habitat structure and abiotic factors has not been explored. Many authors have made reference to macrophytes in the Amazon floodplain as important habitat for shelter and food for young fishes (Saint-Paul and Bayley, 1979; Goulding, 1980; Bayley, 1983; Junk, 1984), and have considered macrophytes as the most important nursery

areas for migratory characiforms. Nevertheless, presence of individual species and the structure of fish assemblages in terms of species composition and relative abundances have not been related to environmental conditions at the microhabitat level and are largely unknown. Studies in the Orinoco and Araguaia basins (Rodriguez and Lewis, 1997; Tejerina-Garro et al., 1998) have shown that floodplain lakes fish assemblages are strongly influenced by water transparency and predation, but found no effect of aquatic macrophytes or other environmental variables in determining fish distribution.

This study describes the characteristics of the spatial distribution of fish species in relation to habitat attributes in a floodplain area of the Amazon River. The objectives of this study were to characterize the distribution of fish species richness in relation to the presence of aquatic macrophytes and habitat structural characteristics as well as other environmental factors. I used canonical correspondence analysis and indicator species values to describe the relative importance of physical and chemical environmental variables in structuring the composition and spatial distribution of young fish assemblages.

Methods

Field sampling

The sampling strategy for this study followed the empirical experience of previous studies in the Amazon floodplain (Bayley, 1983; Junk et al., 1983). The aquatic environment of the floodplain continuously changes while the

water rises and falls during the flood cycle. Spatial expansion and contraction of habitats and the continual movement of habitat edges during flooding presents problems for the application of standard random sampling procedures. For example, randomly selected fixed-point sampling sites are inadequate because they do not take into account available fish habitats change when located in the floodplain during the flood cycle. Young fishes tend to move inward into the floodplain while water is rising. In floodplain systems, water depth is a more important factor in defining fish habitat than fixed geographic locations, and was therefore used as a key stratification criterion for selecting representative samples within geographic zones. To represent the variability of environmental condition and diversity of habitats within the floodplain, my sampling strategy took into account three basic elements on a hierarchical basis: depth, vegetation characteristics and geographic location.

Five geographical areas within Marchantaria Island were selected as follows: southeastern shallows (area A1) from 50 – 500 m to the main channel; the bay in front of Lake Camaleão (area A2) 200 to 500 meters from the main channel; northeastern shallows (area A3) 200m to 1.5 km from the main channel; bottom of lower bay (area A4) 1.5 - 2.0 km from the main Channel; and Lake Camaleão (area A5) 2.5 - 3 km from the main channel (Fig. 2.1). Four to six samples were collected in each area during each of seven sampling trips. Water depth and macrophytes attributes were used to define sampling locations within each of the 5 geographic areas. Inshore

shallow areas with less than 2 meters of depth were sampled more intensively than deeper offshore areas.

Seven vegetation strata were defined and sampled, based on the common emergent aquatic macrophytes. Three strata were predominantly aquatic grasses, *Echinochloa polystachya* (canarana=CAN), *Paspalum repens* (membeca=MEM), and *Panicum sp* (PAN). Two strata were free-floating species; *Eichhornia crassipes* (EIC) and *Pistia stratiotes* (PIS). These tend to be the dominant emergent aquatic macrophytes in the Amazon floodplain throughout the hydrologic cycle (Junk, 1970). The sixth stratum was the semi-aquatic *Paspalum fasciculatum* (murim=MUR), which was sampled late in the flood cycle when suitable stands became flooded. The seventh stratum was in open water free of vegetation (UNV). Sampling could not be performed inside the flooded forest.

Data were collected during seven 5-day field trips carried out every two weeks between the first week of January and the first week of April, 1993 (139 samples). This time period was chosen because it coincides with the first 4 months of the 6-month flooding season, when most fish invade the newly flooded areas. It is also during the reproductive period for many species that use the flooded areas as nursery. A minimum of twenty samples was collected per trip except during the last trip when only 15 suitable sampling sites could be located. No samples could be exactly replicated due to seasonal changes of water depth and macrophyte-type combinations. I attempted to obtain at least one sample from each vegetation strata from each

geographic area. When one or more strata were missing from an area, sampling effort was redistributed according to dominant strata existing at the time.
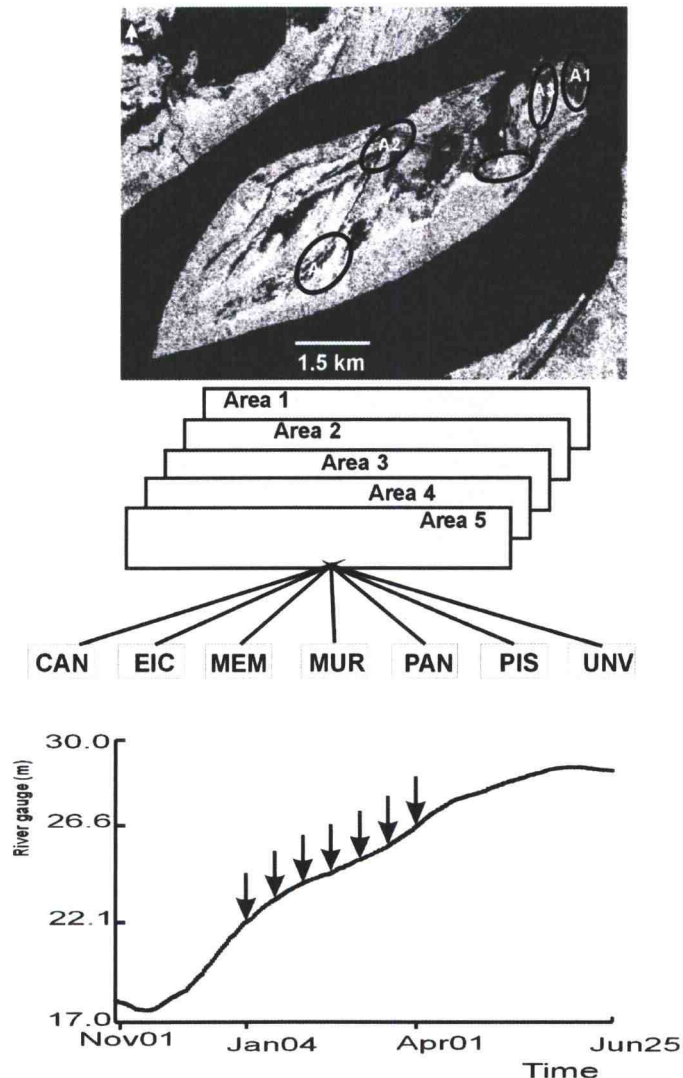
Figure 2.1. Marchantaria Island SAR image (Nasda Jers-1) showing the 5 geographic areas sampled. Southeastern shallows (A1), bay in front of Lake Camaleão (A2), northeastern shallows (A3), Bottom of lower bay (A4) and Lake Camaleão (A5); sampling design and temporal sampling effort in relation to the flood cycle (arrows indicate sampling dates). River flows from left to right.

Samples were separated by a minimum of 200 m if sampled on the same day, or were sampled after at least 24 hs apart if closer than 200 m.

During the first day of each trip, I selected sampling sites based on the stratified design, with the criteria for suitability for gear operation and accessibility. Sampling sites often had to be prepared by opening a trail through the vegetation to allow the canoe to lay the net. Prior to sampling, I recorded sample location, date, time, distance to shoreline (visual estimate), air temperature, water temperature at the surface and bottom, transparency (Secchi disk reading), electrical conductivity (μS/cm), dissolved oxygen at the surface and bottom (mg/l) and H_2S (mg/l) near to bottom. Water conductivity and dissolved oxygen were measured with conductivimeter (American Marine Inc. model Pinpoint) and YSI model 57 oxymeter respectively; H_2S was measured using a colorimetric method (LaMotte SL-P70 test kit). A photograph of the net deployment at the site was also taken. Taxonomic composition of aquatic macrophytes, percentage of dominant and sub-dominant vegetation types and percentage of vegetation coverage of the area sampled were recorded.

A ranked measure was used to describe the degree of habitat complexity of each site. Each rank on the scale 0-5 was defined qualitatively, based on presence of vegetation type, compactness of the stands and complexity of stems and root structure as follows:

0- Pelagic zone with no vegetation, absence of any structural characteristics;

1- Aquatic macrophytes present, stems rooted to the ground standing throughout the water column in low density, low compactness, characterized by stands of murim and canarana;

2- Aquatic macrophytes present, stem structure rooted to the ground standing throughout the water column, in moderate density and moderate to high compactness, characterized by mature stands of canarana;

3- Aquatic macrophytes present, stems rooted to the ground standing throughout the water column in high density and high compactness, characterized by stands of *Panicum sp*;

4- Floating macrophytes without stems but with complex reticulated root structure that extends up to 1 meter deep standing in the water column in moderate to high density, high compactness, characterized by stands of *Eichhornia crassipes* and *Pistia stratiotes*;

5- Floating and rooted macrophytes with stems rooted to the ground standing throughout the water with complex reticulated root structure attached to the emergent layer that extends more than 1 meter deep and secondary roots the are attached to the stems, standing in the water column in high density, high compactness, dominated by stands of *Paspalum repens* usually in combination with other macrophytes.

Standardized samples were taken using a calibrated 25 m X 6 m seine net with 5 mm mesh size as described in Bayley, 1983. At the sampling site, the net was deployed from the middle of a paddle-powered canoe encircling an area varying from 49 to 70 m^2. Two basic net operations were used. At

sites less than 1.5 m depth the net was deployed in a circle with the lead line on the bottom (Fig. 2.2). If enclosed by the net, vegetation was removed manually, prior to retrieving the net (fishing method C described in Bayley, 1983).

Figure 2.2. Net deployed in a circle with the lead line on the bottom, fishing method C (Bayley 1983).

At sites greater than 1.5 m water depth, the net was operated as a lampara net (fishing method A described in Bayley, 1983). The net was deployed similarly to the previous method, however, the lead line was pulled directly into the canoe and vegetation retained in the net was removed after the lead line had been fully retrieved to the canoe (Fig. 2.3). The netting containing the debris was held in the water, and small portions retrieved on board and

carefully inspected for small fish. Most fish were preserved in 10% buffered formalin, but all small (below 100 mm SL) serrasalmins were preserved separately in 95% ethanol to better preserve otoliths. Larger specimens were identified in the field, measured to the nearest millimeter (SL and FL) and weighed before being discarded.

Figure 2.3. Net operated as a lampara net, the lead line was pulled directly into the canoe, fishing method A (Bayley 1983).

Retained specimens were identified in the lab, measured and transferred to 70% ethanol for final storage. Voucher specimens are deposited at the fish collection of the National Institute for Amazon Research (INPA) in Manaus.

In addition to the 139 samples collected as described above, I used original unpublished data from a subset comprising 229 samples collected by P.B. Bayley from Marchantaria Island, Janauacá area and Janauarí area between 1977, 1978 and 1979 during the flooding season (Nov. – May). A second subset of 205 samples from year round samples (1977-79) only from Marchantaria Island was also used

Quantitative analysis

Raw catch data were converted to CPUE (number of fish caught per haul per 70 m^2). The resulting data were then arranged into a species (139 used) by sample matrix (139X139), and transformed as $\log_e (x+1)$ in order to help homogenize variances. Species-accumulation curves were used as an approximate method to compare fish species diversity in this study and (Bayley, 1983)data for the same study area. The curve for Bayley's data was computed using information from 205 samples collected year around between 1977 and 1979 at Marchantaria Island. Both species-accumulation curves and first and second order jackknife species richness estimators (Palmer, 1990; Palmer, 1991) were computed with PC-ORD V. 3.14 (McCune and Mefford, 1997).

Vegetation coverage variables, expressed in percentages, were transformed as arcsine (p) to approach normal distributions (Zar, 1984). The effects of water quality parameters and vegetation characteristics on sample

species richness (number of species caught) and fish numbers $\log_e$ (CPUE+1) were analyzed by multiple regression analysis. A forward step-wise procedure was used to select the best subset of explanatory variables. A one-way ANOVA was used to test the effect of vegetation strata and sampling area on species richness, using Statgraphics V.7.0. Results were assessed at the Bonferroni-corrected 5% rejection level. Species richness among vegetation strata was also analyzed using the rarefaction technique (Hurlbert, 1971; Gotelli and Graves, 1996) to adjust the number of species captured for differences in number of individuals caught (Benson and Magnuson, 1992). Species rarefaction curves for each stratum were based on random sub sampling of individuals. Estimated species number (E_{Sn}) was computed for 1000 individuals for all strata except for the unvegetated stratum, for which computation was done on 500 individuals due to small sample size. Rarefaction curves were computed using a customized version of RAREFRAC.BAS (Ludwig and Reynolds, 1988).

Direct gradient analysis

From the original species by sample matrix, a reduced matrix with 76 of the 139 species of fish was used to analyze the structure of fish assemblages in relation to environmental gradients. Species retained occurred in a minimum of 5% (>7) samples. Rare species would not contribute significant weight to the analysis and were therefore eliminated to clarify interpretation.

The null hypothesis of no relationship between the fish CPUE matrix and the environmental variables matrix was evaluated by the Mantel test (Mantel, 1967). Euclidean distance was used as the dissimilarity measure, and the critical p value was calculated by a randomization (Monte Carlo) test with 1000 permutations using PC-ORD V.3.14b (McCune and Mefford, 1997).

Fish assemblage structure was analyzed by direct gradient analysis using Canonical Correspondence Analysis (CCA; (Ter Braak, 1986), as implemented in CANOCO V. 3.10, (Ter Braak, 1990) and PC-ORD V.3.14b (McCune and Mefford, 1997). This technique allows the simultaneous representation of sample sites, environmental variables and species centroids in a reduced ordination space of orthogonal axes. CCA is an eigenvector ordination technique for analysis of relationships among multivariate ecological data. CCA provides an integrated quantification of species-environment relationships by assuming a common response (unimodal distribution) of all species to a set of underlying environmental gradients (Ter Braak, 1986).

Environmental variables were selected by a stepwise forward procedure analogous to multiple regression analysis by selecting the minimum set of variables that explain the species data. This procedure is based on a Monte Carlo permutation test for the sum of all eigenvalues to evaluate the statistical significance of each variable (Ter Braak, 1990). A 5% significance level was used as the cut-off point to reject a variable in the model.

The significance of relationships between fish distribution and environmental gradients were based on a Monte Carlo permutation test (1000 permutations) for the sum of all eigenvalues, as well as for the first three canonical axes. Axis scores were standardized by centering and normalizing to unit variance, and the scale was optimized so that species scores were weighted mean site scores and the inter-species distances approximate their chi square distances, (Ter Braak, 1990). Species points are at the centroid of the samples in which they occur, and are the weighted average of the projection points of the samples with respect to environmental variables (McCune and Mefford, 1997). This allowed a direct spatial interpretation of the relationship between environmental and species points. The relationship between ordination axes and environmental variables was evaluated by a t test of significance for the canonical coefficients of each variable and the inter-set correlations.

Ordination biplot diagrams were computed using site scores as linear combinations of environmental variables (LC scores) as recommended by (Ter Braak, 1994; Ter Braak and Verdonschot, 1995; McCune and Mefford, 1997). Environmental arrows point in the direction of maximum change in the value of the associated variable, and the coordinates of the arrow head are correlations with the axes; the length is equal to the size of the effect that the corresponding variable has on the ordination scores while neglecting other variables (Ter Braak, 1994). Ordination biplots of species + environmental variables and sites + environmental variables were plotted with canodraw

V.3.0 lite (Smilauer, 1992). Species abundance and environmental variables values were plotted using raw scores overlaid on to the ordination space as implemented in PC-ORD V.3.14b. To analyze the distribution of species in the ordination space in relationship to trophic guilds, species were classified into the following trophic groups: detritivores, lepidovores, planktivores, omnivores, piscivores and insectivores, and replotted on to the ordination space.

<u>Indicator species analysis</u>

Indicator species analysis (Dufrêne and Legendre, 1997) was used to describe the relationship between the 76 species included in the CCA and samples grouped by vegetation strata. This method combines species abundance and the faithfulness of occurrence of each species in each group, providing an indicator value for each species in each group. Sampling sites were also classified according to dissolved oxygen concentrations to relate species distribution to environmental conditions. Oxygen concentration thresholds were defined after Saint-Paul and Soares, (1987). Sites were coded as hypoxic with less than 1 mg/l, intermediate with 1-2 mg/l and oxygenated with more than 2mg/l. The significance of the indicator values was tested using a Monte Carlo technique (McCune and Mefford, 1997).

Results

Water physico-chemical parameters

Water temperature at the surface ranged from 26.9 to 34.5 °C; dissolved

oxygen from 0.05 to 7.2 mg/l; electrical conductivity from 65 to 173 μS/cm;

hydrogen sulphide from 0 - 0.5 mg/l and water transparency from 15 to 85 cm.

There were no significant differences in water physico-chemical

characteristics among the seven vegetation strata, but significant differences

were detected among the five geographical areas sampled in Marchantaria

Island. Water temperature was significantly higher in the shallow, clear and

stagnant water of area 4 (Fig. 2.4a) (F= 6.82; p=0.0001), dissolved oxygen

was higher for areas 1, 2, and 3 (Fig. 2.4b) (F=6.54, p=0.0001), electrical

conductivity significantly higher in areas 1, 4 and 5 (Fig. 2.4c) (F= 5.3,

p=0.0005), and water transparency higher in areas 4, 5 (Fig. 2.4d) (F= 18.03,

p=0.0000). These results largely reflected the geographic locations of the five

sampling areas within the island. Areas 1, 2, and 3 were located close to the

island margin, directly influenced by river water inflow, and the water was

cooler, turbid and oxygenated. Areas 4 and 5 were located deep into the

island (Fig. 2.1), had no direct influence from river water inflow during the

entire sampling period, and were warm, clear, hypoxic and stagnant.
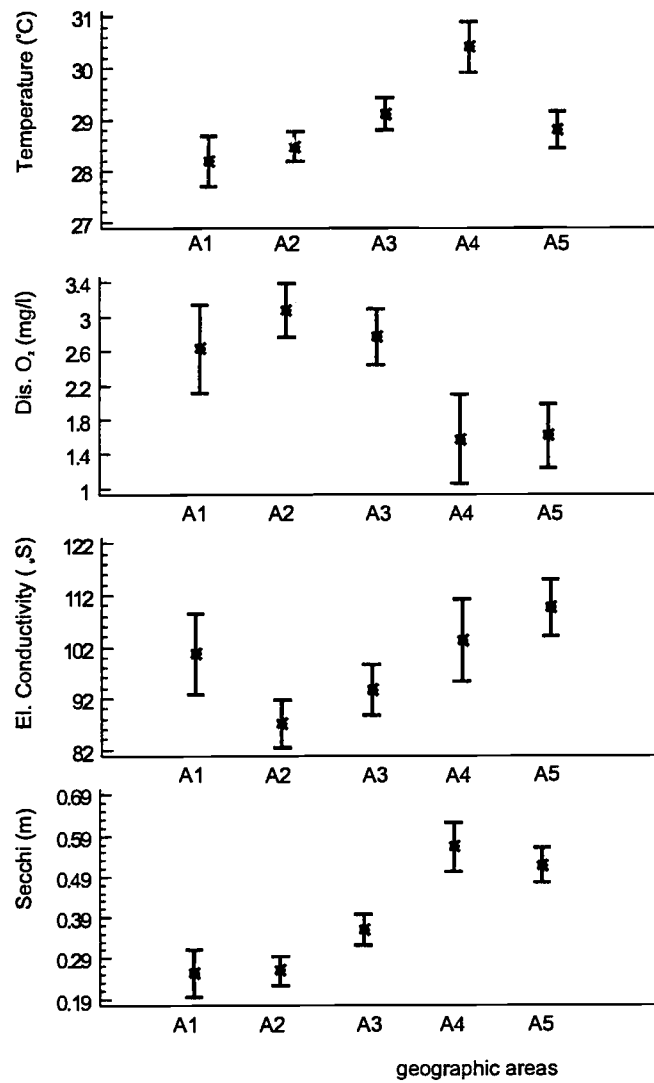
Figure 2.4. ANOVA mean plots and 95% Bonferroni confidence intervals of water physico-chemical parameters for the five areas sampled in Marchantaria Island.

Species composition

A total of 25,819 specimens representing 8 orders, 30 families, 101 genera and 139 species of fish were collected (Table 2.1). Ostariophysan fishes were the most diverse group with 116 species, 83.6% of total species richness. Characiformes with 8 families, 42 genera and 63 species dominated with 45% of the total species and 87.8 % of the total number of specimens captured. Other important ostariophysans were Siluriformes (10 families, 26 genera and 31 species), representing 22.1% of species, but only 6.1% of specimens; and Gymnotiformes (5 families, 13 genera and 22 species) representing 16.5% of species, but only 0.7% of specimens. Important non-ostariophysan fishes were Perciformes (2 families, 13 genera and 13 species representing 9.3% of species, and 4.38 % of specimens) and Clupeiformes (2 families, 5 genera and 7 species representing 5.0 % of species and 0.57% of specimens). The remaining orders Lepidosireniformes, Synbranchiformes and Tetraodontiformes were each represented by one species, of which only Synbranchiformes were captured in significant numbers.

Within Characiformes, Characidae (35 species), Curimatidae (13 species) and Anostomidae (6 species) were the most diverse families. Among Siluriformes, the most diverse group present in the samples was Pimelodidae with 9 species, followed by Doradidae with 5 species; Ageneiosidae,

Table 2.1. Summary of species occurrence, number of specimens and presence/absence in catch for each vegetation strata sampled at Marchantaria Island. Strata were: CAN (canarana), EIC(*Eichhornia*), MEM (membeca), MUR (murim), PAN (*Panicum*), PIS (*Pistia*) and UNV(unvegetated).

Taxonomic rank	Presence	Catch	Strata						
Order	N°samples	N°specimens	C A N	E I C	M E M	M U R	P A N	P I S	U N V
Family (No. Of species)									
Species										
LEPIDOSIRENIFORMES									
Lepidosirenidae (1)									
Lepidosiren paradoxa	1	1			+				
CLUPEIFORMES									
Engraulidae (3)									
Anchovia surinamensis	13	42		+	+		+•	+•	+
Lycengraulis batesi	5	11	+						+
Lycengraulis grossidens	3	6			+		+		+
Pristigasteridae (4)									
Ilisha Amazonica	3	4		+	+				+
Pellona castelnaeana	22	41	+	+	+		+	+	
Pellona flavipinnis	11	27		+	+		+	+	
Pristigaster cayana	9	17		+	+		+•		
CHARACIFORMES									
Anostomidae (6)									
Laemonita proximus	22	77	+	+	+	+	+		
Laemonita taeniata	55	268	+	+	+	+•	+		+
Leporinus friderici	32	125	+		+		+	+	
Rhythiodus argenteofuscus	1	2			+				
Rhythiodus microlepis	40	140	+	+•	+	+•	+		+
Schizodon fasciatus	63	349	+	+	+	+	+	+•	
Characidae(35)									
Acestrorhynchus sp	1	3	+						
Agoniates anchovia	7	7	+	+	+				+
Aphyocharax alburnus	55	316	+	+	+	+	+	+	+
Brycon erithropterus	30	262	+	+	+	+	+	+	+
Brycon melanopterum	7	32	+		+	+		++	
Charax hemigrammus	15	82	+	+	+		+	+	
Charax stenopterus	8	11	+		+		+		
Cheirodon piaba	65	861	+	+	+	+	+	+	+
Colossoma macropomum	17	47							

Table 2.1. continued

Taxonomic rank	Presence	Catch	Strata						
Order	N°samples	N°specimens	C A N	E I C	M E M	M U R	P A N	P I S	U N V
Family (No. Of species)									
Species									
Ctenobrycon hauxwellianus	96	2616	+	+	+	+	+	+	+
Eucynopotamus biserialis	12	32	+	+	+	+			+
Galeocharax gulo	1	2		+					
Hemigrammus bellottii	5	40	+		+				
Hyphessobrycon calisticus	37	333	+	+	+	+	+	+	+
Hyphessobrycon erythrurus	2	8			+				+
Hyphessobrycon sp2	22	130	+	+	+			+	+
Hyphessobrycon sp3	4	40	+		+				
Hyphessobrycon sp4	17	139		+	+	+	+	+	
Iguanodectes purusi	1	1					+		
Moenkhausia intermedia	76	1434	+	+	+	+	+	+	+
Moenkhausia lepidura	24	264	+	+	+	+	+		+
Myleus sp	1	6			+				
Mylossoma aureum	126	2660	+	+	+	+	+	+	+
Mylossoma duriventri	102	1293	+	+	+	+	+	+	
Odontostilbe fugitiva	32	202	+	+	+		+		+
Piaractus brachipomus	28	118	+	+	+	+	+	+	+
Pygocentrus nattereri	75	469	+	+	+	+	+	+	
Roeboides meyeri	5	21	+		+				
Roeboides thurni	37	358	+	+	+	+	+	+	+
Serrasalmus elongatus	1	1			+				
Serrasalmus rhombeus	57	250	+	+	+	+	+	+	+
Serrasalmus spiropleura	26	66							
Tetragonopterus sp	2	3	+			+			
Triportheus angulatus	45	250	+	+	+	+	+	+	+
Triportheus elongatus	79	1022	+	+	+	+	+	+	+
Curimatidae (13)									
Curimatella meyeri	4	6	+•		+				
Cyphocharax spilurus	3	3	+		+	+			
Potamorhina latior	16	81	+	+	+	+	+		+
Potamorhina pristigaster	2	5			+		+		
Potamorhina sp	21	467	+	+	+	+	+		
Potamorhyna altAmazonica	2	7			+				
Psectrogaster Amazonica	16	112	+		+	+	+	+	+
Psectrogaster rutiloides	17	890	+	+	+	+	+		+
Psectrogaster sp	29	3912	+		+	+	+		+
Steindachnerina argentea	2	5	+		+				
Cynodontidae (3)									
Cynodon gibbus	2	3		+	+				
Hydrolicus scomberoides	12	24	+	+	+	+	+		
Rhaphiodon vulpinus	59	251	+	+	+	+	+	+	+

Table 2.1. Continued

Taxonomic rank	Presence	Catch	Strata						
Order	N°samples	N°specimens	C A N	E I C	M E M	M U R	P A N	P I S	U N V
Family (No. Of species)									
Species										
Erythrinidae (1)									
Hoplias malabaricus	55	201	+	+	+	+	+	+	+
Hemiodontidae (1)									
Eigenmanina melanopogon	22	338	+	+	+	+	+	+	
Lebiasenidae (1)									
Pyrrhulina sp	8	11	+		+				
Prochilodontidae (3)									
Prochilodus nigricans	24	62	+	+	+	+	+		+
Semaprchilodus insignis	43	1267	+		+	+	+	+	+
Semaprochilodus taeniurus	45	642	+		+	+	+		+
GYMNOTIFORMES									
Apteronotidae (9)									
Adontosternarchus sp	1	1			+				
Apteronotus bonaparti	7	12	+		+			+	
Apteronotus hasemani	14	30	+	+	+		+	+	
Apteronotus sp	9	29		+	+			+	
Porotergus compsus	3	7	+		+		+		
Sternarchella orthos	2	2			+	+			
Sternarchella terminalis	2	2		+	+				
Sternarchogiton nattereri	8	15	+	+	+		+		
Sternarchorhynchus sp	4	4			+				
Gymnotidae (2)									
Gymnotus anguillares	1	1			+				
Gymnotus stenoleucus	6	8	+	+	+			+	
Hypopomidae (5)									
Brachyhypopomus brevirostris	1	1			+				
Brachyhypopomus sp	5	11	+	+				+	
Hypopomus cf artedii	3	7	+	+				+	
Hypopomus sp	1	1			+				
Steatogenis elegans	6	11	+		+			+	
Rhamphichthyidae (2)									
Rhamphichthys rostratus	3	3			+				
Rhamphichthys sp2	1	1			+				
Sternopygidae (4)									
Distocyclus conirostris	3	7			+	+			
Eigenmannia humbolti	2	8			+	+			
Eigenmannia macrops	6	16			+	+	+		
Eignmannia sp	7	9	+	+	+			+	

Table 2.1. Continued

Taxonomic rank Order Family (No. Of species) Species	Presence N°samples	Catch N°specimens	Strata CAN	EIC	MEM	MUR	PAN	PIS	UNV
SILURIFORMES									
Ageneiosidae (3)									
Ageneiosus dentatus	10	13	+	+	+				
Tympanopleura sp1	3	4		+	+				
Tympanopleura sp2	3	3		+	+				
Auchenipteridae (3)									
Auchenipterus nuchalis	10	22		+	+				
Centromochlus heckelii	15	36		+	+	+	+		+
Parauchenipterus galeatus	11	20		+	+		+		
Bunocephalidae(1)									
Bunocephalus sp	1	1	+						
Callichthyidae (3)									
Coridoras hastatus	25	124	+		+	+	+		
Hoplosternum litoralli	6	10			+	+	+		
Hoplosternum thoracatum	10	22	+		+	+	+		
Cetopsidae (1)									
Hemicetopsis candiru	1	1			+				
Doradidae (5)									
Doras microstomus	5	6		+	+				
Opsodoras sp1	1	1				+			
Pseudodoras niger	1	1							
Pterodoras granulosus	2	4			+				
Trachidoras sp	10	35		+	+		+	+	
Hypophthalmidae (2)									
Hypophthalmus fimbriatus	4	7		+	+				
Hypophthalmus marginatus	14	34		+	+			+	
Loricariidae (3)			+		+		+		
Hypostomus plecostomus	3	14	+	+					
Liposarcus pardalis	73	712	+	+	+	+	+	+	+
Pimelodidae (9)									
Leiarius marmoratus	3	3			+	+			
Phractocephalus hemiliopterus	1	1			+				
Pimelodella sp	6	7		+	+				
Pimelodus altissimus	1	1			+				
Pimelodus blochi	61	364	+	+	+	+	+	+	
Pinirampus pirinampu	3	5		+	+				
Pseudoplatistoma sp1	16	28	+		+			+	
Pseudoplatistoma sp2	4	6				+		+	
Sorubim lima	19	32	+	+	+	+	+	+	
Thichomicteridae (1)									
Apomatocerus alleni	1	1			+				

Table 2.1. Continued

Taxonomic rank	Presence	Catch	Strata						
Order	N °samples	N °specimens	C A N	E I C	M E M	M U R	P A N	P I S	U N V
Family (No. Of species)									
Species									
PERCIFORMES									
Cichlidae (12)									
Acarichthys heckelii	20	100	+	+	+	+	+		
Apistogramma sp	1	1	+						
Astronotus ocelatus	8	37	+	+	+				
Chaetobranchopsis orbicularis	10	32	+	+	+	+	+	+	
Chaetobranchus flavecens	2	7				+			
Cichla monoculus	11	15	+		+		+	+	
Cichlasoma Amazonarum	84	913	+	+	+	+	+	+	+
Crenicichla labrina	6	7	+		+	+			
Geophagus surinamensis	1	2	+						
Mesonauta insignis	9	12	+	+	+			+	
Pterophylum scalarae	1	1	+						
Satanoperca jurupari	7	21	+		+	+			+
Sciaenidae (1)									
Plagioscion sp	1	3				+			
SYNBRANCHIFORMES									
Synbranchidae (1)									
Synbranchus marmoratus	30	89	+	+	+			+	
TETRAODONTIFORMES									
Tetraodontidae (1)									
Colomesus psitacus	10	14		+	+		+		

Auchenipteridae, Callichthyidae and Loricariidae with 3 species each;

Hypophthalmidae with 2 species and Bunocephalidae, Cetopsidae and

Trichomicteridae with one species. Gymnotiformes were composed of 9

species of Apteronotidae, 6 species of Hypopomidae, 4 species of

Sternopygidae and 2 species of Gymnotidae and Rhamphichthyidae.

Perciformes were composed of Cichlidae with 12 species, and Sciaenidae

with only one species. Clupeiformes were represented by 4 species of Pristigasteridae and 3 species of Engraulidae.

Species richness of the catch at a site ranged from 1 to 35 and fish number caught from 1 to 2463. There was a significant difference in mean species richness among sampling areas. Area 2 had significantly higher mean richness (F-ratio=7.11, p=0.0000) than the other four areas (Fig. 2.5a).A linear regression analysis showed a weakly significant relationship ($R^2 = 0.78$, F-ratio= 10.71, p= 0.046) between mean species richness and the proportion of Membeca samples in an area (Fig. 2.5b).

The species-accumulation curve and total diversity estimates were similar to Bayley (1983) (Fig. 2.6a). For my data the observed number of species reaches the asymptote after 125 samples had been added to the data pool, whereas for Bayley's data set the asymptote was reached at 150 samples. Total species richness based on first and second order jackknife estimators are presented in table 2.2.

Many species were rare with 25 (17.8%) occurring once, and 66 species (47.1%) occurring in less than 5% of the samples. Of the more frequent species, 26 (18.7%) occurred in 5 - 10% of samples, 21 (15.1%) occurred in 10 - 20%, 19 (13.7%) in 20 - 50% of samples, and only 8 species (5.7%) were present in more than 50% of samples.

Table 2.2 Comparative estimates of species richness for Marchantaria Island using first and second order Jackknife estimators, for this study and Bayley's 1983 data.

Estimates for current study (1993)
Estimates of total number of species:
Number of samples = 139
Number of species observed = 139
First-order jackknife estimate of species richness = 164
Second-order jackknife estimate of species richness = 178
Additional information used for jackknife estimates:
Number of columns in matrix with no positive values = 0
Number of species with only 1 occurrence = 25
Number of species with only 2 occurrences = 11

Estimates for Bayley 1983 data for Marchantaria Island samples (year round, 1978-79)

Estimates of total number of species:
Number of samples = 205
Number of species observed = 153
First-order jackknife estimate of species richness = 185
Second-order jackknife estimate of species richness = 204
Additional information used for jackknife estimates:
Number of columns in matrix with no positive values = 0
Number of species with only 1 occurrence = 33
Number of species with only 2 occurrences = 14
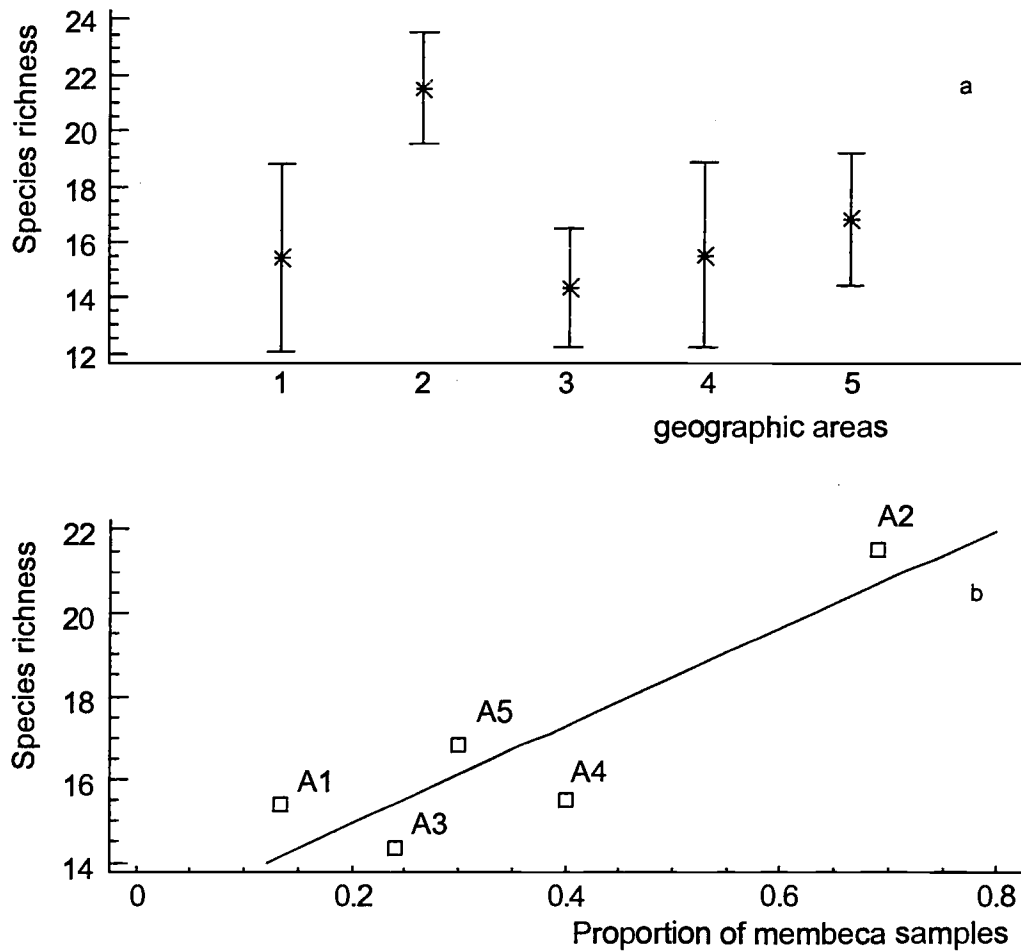
Figure 2.5. ANOVA means plot and 95% Bonferroni confidence intervals for the effect of geographic area on species richness.(a); linear regression model fit for the effect of proportion of membeca samples per geographic area on species richness (b).

Species composition by vegetation strata

Species composition differed among vegetation strata (Table2.1). The total number of species collected in each stratum was: membeca - 121, canarana - 84, *Eichhornia* - 76, *Panicum* - 65, murim - 54, *Pistia* - 53 and

open water 39 (Table 2.3). Estimated species richness E $(_{Sn})$ based on

rarefaction curves for each stratum were membeca - 76, *Eichhornia* - 73,

canarana -61, *Pistia* - 48, *Panicum* - 47, murim - 37 and open water 32

(underestimated because of low catches) but estimate should be in the same

order as murim (Fig. 2.6b).

Table 2.3. Number of species caught per sample by vegetation strata: (CAN)
canarana, (EIC) *Eichhornia*, (MEM) membeca, (MUR) murim, (PAN) *Panicum*,
(PIS) *Pistia* and (UNV) unvegetated.

	CAN	EIC	MEM	MUR	PAN	PIS	UNV
Sample size	23	15	55	9	16	10	11
Median	15	16	19	17	16.5	15	6.5
Minimum	6	6	6	6	6	5	2
Maximum	28	25	32	19	24	20	14
Lower 25% quartile	11	13	17	11	11.5	13	3
Upper 25% quartile	23	18	24	17	18.5	17	8
Total richness	84	76	121	54	65	53	39

The relationship of vegetation strata to fish species richness was

significant and revealed that unvegetated open water sites had significantly

lower species richness than vegetated sites (ANOVA, p=0.0001). On average

Membeca sites had higher number of species (Fig. 2.7), but statistically

significant differences (p<0.05) were only found between Membeca and

Panicum or unvegetated sites (Table 2.4). The pattern was congruent with

results obtained from Bayley's (1983) data for three floodplain areas in the

vicinity of Manaus (Table 2.5). Vegetated areas consistently had higher

species richness when compared to unvegetated areas for two out of the

three areas studied (Fig. 2.8). Bayley's data for Marchantaria Island also

showed the tendency for membeca stratum to have a higher number of

species, but the differences were not statistically significant.
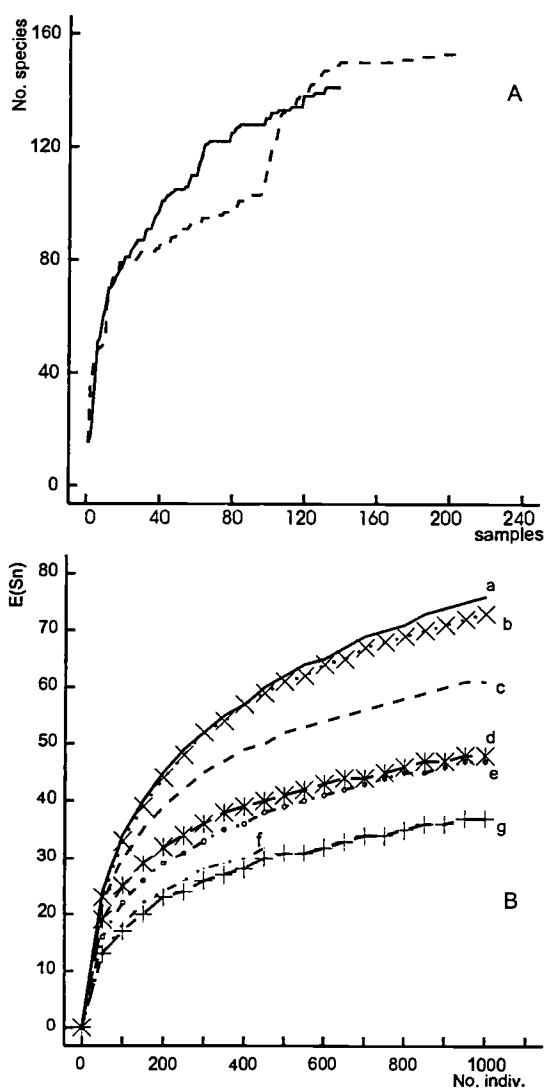
Figure 2.6. (A) Species-area curves showings the observed cumulative species composition across all samples from Marchantaria Island for this study (solid line) and Bayley 1982 study (dashed line). (B), rarefaction curves of expected number of species (E (Sn)) for the vegetation strata; (a) Membeca, (b) Eichhornia, (c) Canarana, (d) Pistia, (e) Panicum, (f) unvegetated and (g) Murim.

Table 2.4. ANOVA table of the effect of vegetation strata on fish species richness, 95% Bonferroni range test.

Source of variation	SS	d.f.	MS	F-ratio	Sig. level	
Between groups	2114.232	6	352.372	10.021	0.000	
Within groups	4606.173	131	35.161			
Total (corrected)	6720.405	137				

Means	N	Ave. No. species	Std. Error (internal)	Std. Error (pooled s)	95 % Bonferroni intervals for mean	
Canarana	23	17	1.60	1.23	14.29	19.70
Eichhornia	15	16.86	1.40	1.53	13.51	20.22
Membeca	55	20.81	0.80	0.79	19.06	22.57*
Murim	9	15.87	1.82	2.09	11.28	20.46
Panicum	16	15.56	1.31	1.48	12.31	18.81*
Pistia	10	15.1	1.46	1.87	10.99	19.20
Unvegetated	11	6.36	1.28	1.78	2.44	10.28*

* Denotes a statistically significant difference
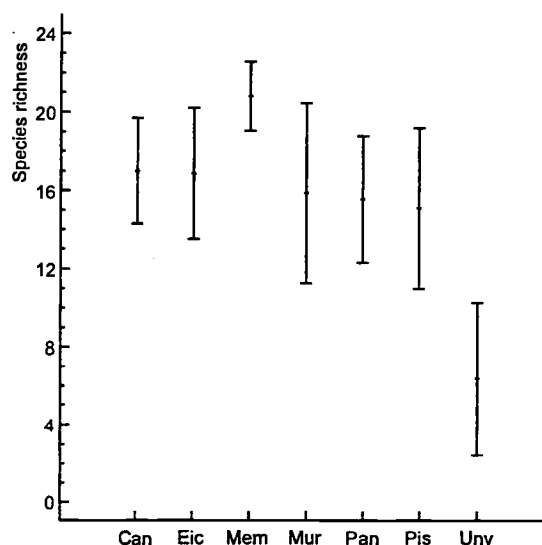
Figure 2.7. ANOVA mean plot and 95% Bonferroni confidence intervals of the effect of aquatic macrophytes on sample fish species richness per vegetation type. Canarana (CAN), Eichhornia (EIC), Membeca (MEM), Murim (MUR), Panicum (PAN), Pistia (PIS) and Unvegetated areas (UNV).

Table 2.5. ANOVA table for the effect of vegetation strata on sample fish species richness for three Amazon floodplain areas, during the flooding season (Nov.-May) between 1977-79. Data from P.B. Bayley unpublished data.

A - Pooled data for the three areas						
Source of variation	SS	d.f.	MS	F-ratio	Sig. level	
Between groups	6236.647	4	1559.162	17.179	0.000	
Within groups	20329.921	224	90.759			
Total (corrected)	26566.568	228				
Means	N	Average	Std. Error	Pooled Error	95 % intervals	
Canarana	19	10.21	1.104	2.186	5.828	14.593
Eichornia	47	20.28	1.368	1.390	17.490	23.063
Membeca	82	21.10	1.194	1.052	18.988	23.207
Soft ter. Veget.	38	20.45	1.663	1.545	17.349	23.546
Unvegetated	43	8.51	1.181	1.453	5.599	11.424
Total	229	17.55	0.630	0.630	16.292	18.817
B- Marchantaria Island						
Between groups	849.272	4	212.318	3.697	0.0091	
Within groups	3617.595	63	57.422			
Total (corrected)	4466.868	67				
Means	N	Average	Std. Error	Pooled Error	95 % intervals	
Canarana	10	9.6	1.477	2.396	4.670	14.530
Eichornia	10	11.3	2.334	2.396	6.370	16.230
Membeca	28	16.11	1.730	1.432	13.161	19.054
Soft ter. Veget.	8	13.75	2.617	2.679	8.238	19.262
Unvegetated	12	6.92	1.469	2.188	2.416	11.417
Total	68	12.54	0.919	0.919	10.653	14.435
C- Janauacá area						
Source of variation	SS	d.f.	MS	F-ratio	0.000	
Between groups	5926.912	4	1481.728	16.077		
Within groups	6267.033	68	92.1623			
Total (corrected)	12193.945	72				
Means	N	Average	Std. Error	Pooled Error	95 % intervals	
Canarana	3	16.33	2.603	5.543	4.960	27.707
Eichornia	6	26.50	4.241	3.919	18.458	34.542
Membeca	31	25.42	2.015	1.724	21.881	28.957
Soft ter. Veget.	11	28.64	3.067	2.895	22.697	34.576
Unvegetated	22	6.68	1.378	2.047	2.482	10.882
Total	73	19.97	1.124	1.124	17.667	22.278
D- Janauarí area						
Between groups	1228.799	4	307.200	4.088	0.0045	
Within groups	6236.644	83	75.140			
Total (corrected)	7465.443	87				
Means	N	Average	Std. Error	Pooled Error	95 % intervals	
Canarana	6	8.17	1.138	3.539	0.949	15.384
Eichornia	31	21.97	1.425	1.557	18.792	25.143
Membeca	23	21.35	2.059	1.807	17.661	25.034
Soft ter. Veget.	19	18.53	1.952	1.989	14.470	22.582
Unvegetated	9	15.11	3.458	2.889	9.218	21.004
Total	88	19.42	0.924	0.924	17.536	21.305

51
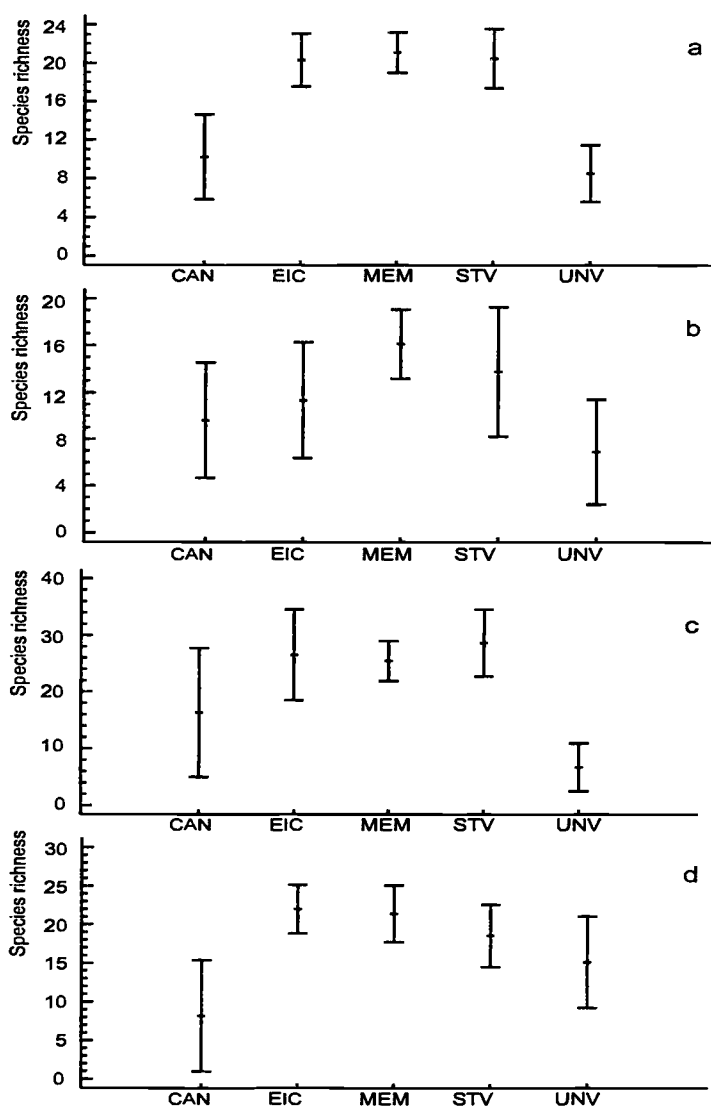
Figure 2.8. ANOVA mean plots and 95% Bonferroni confidence intervals for the effect of vegetation cover on samples fish species richness for 3 areas in the Amazon floodplain. Pooled data from all 3 areas (a), Marchantaria Island (b), Janauacá area(c), and Janauarí area (d). Vegetation cover types are canarana (CAN), *Eichhornia* (EIC), membeca (MEM), soft terrestrial vegetation (STV) and unvegetated (UNV). P.B.Bayley' s unpub. data.

The influence of water physico-chemical parameters and vegetation characteristics on sample species richness was analyzed by stepwise regression. Because of significant correlations among variables only a subset was initially entered into the model (depth, dissolved oxygen, water temperature, hydrogen sulphide concentration and habitat complexity). Only habitat complexity had significant positive effect on sample species richness (Fig. 9, Table 2.6). The effects of environmental variables on the catch per sample (Log_e(CPUE+1)) was also analyzed using a stepwise regression. As in the previous analysis, habitat complexity had significant positive effect. In addition, dissolved oxygen and water depth had significant negative effects, and Hydrogen sulphide had positive effect (Table 2.7, Fig. 2.10).

Table 2.6. Stepwise regression of the effect of environmental variables on species richness of the catch per sample. Results report only the variables retained in the model after 1 step.

Ind. Variable	coefficient	Std. Error	t-value	sig.level	
Constant	10.3982	1.21	8.57	0.0000	
Hab. Complexity	2.00	0.31	6.29	0.0000	
Analysis of Variance for the Full Regression					
Source	SS	DF	MS	F-Ratio	P-value
Model	1506.62	1	1506.62	39.57	0.0000
Error	5215.44	137	38.06		
Total (Corr.)	6722.06	138			
R-squared =	022				
St.error est. =	6.17				
R-squared (Adj. for d.f.) =0.21					
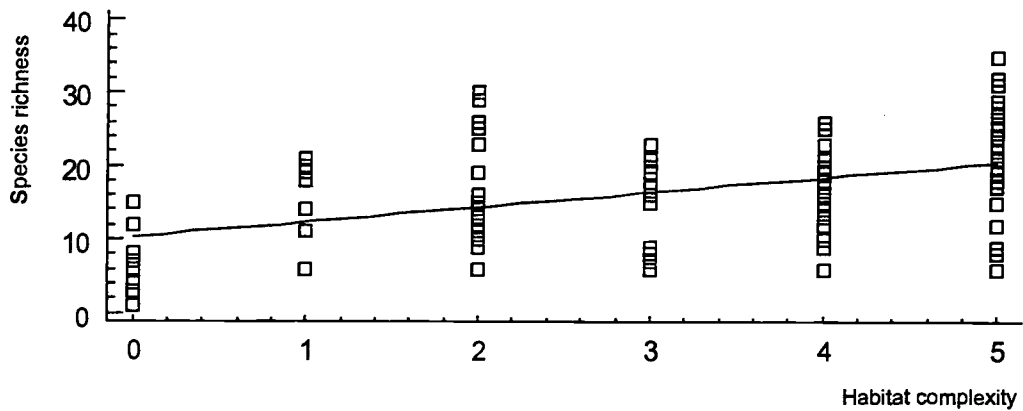
Figure 2.9. Stepwise regression plot of the effect of habitat complexity on sample species richness.

Table 2.7. Stepwise regression table of the effect of environmental variables on fish catch per sample ($\log_e(CPUE+1)$). Results report only the variables with significant effect retained in the model after 4 steps.

Ind. Variable	coefficient	std. Error	t-value	sig.level	
Constant	5.104	0.200	1.217	0.2256	
Hab. Complexity	0.341	0.050	4.290	0.0000	
D.O$_2$	-0.223	0.048	-4.629	0.0000	
Depth	-0.379	0.065	-5.856	0.0000	
H$_2$S	1.271	0.468	2.713	0.0075	
Analysis of Variance for the Full Regression					
Source	SS	DF	MS	F-Ratio	P-value
Model	61.520	4	15.380	21.113	0.000
Error	97.615	134	0.728		
Total (Corr.)	159.136	138			
R-squared =	0.386				
St.error est. =	0.853				
R-squared (Adj. for d.f.) =0.368					
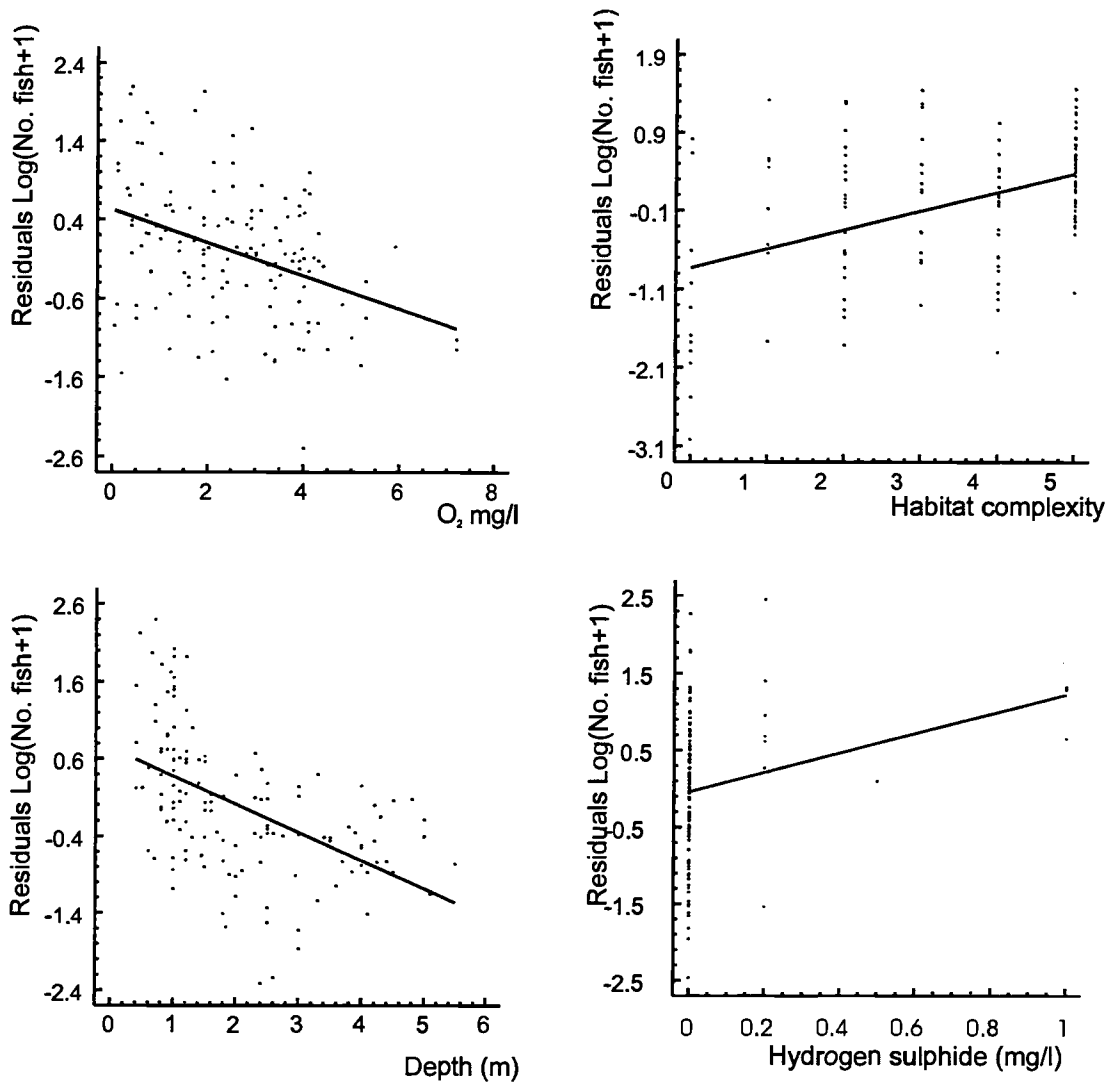
Figure 2.10. Stepwise regression residual plots for the partial components effects of the environmental variables with significant effect on fish catch per sample ($\log_e$(CPUE+1).

Direct gradient analysis

The Mantel test based on the Ln transformed CPUE matrix (76X139)

and the environmental variables matrix (14X139) was used to evaluate the

association between the two matrices. The test detected a strong relationship (p=0.006) between the two matrices after 1000 permutations. This indicates that there is a strong relationship between fish assemblage structure and environmental variables (Table 2.8). The Mantel test also showed that there was no strong autocorrelation in fish numbers per site, indicating that sampling sites were spatially independent, fulfilling an important assumption of the statistical test of relationship between environmental variables and assemblage structure (Hinch et al. 1994).

Table 2.8. Mantel null model significance test for association between CPUE per species per sample and environmental variables per sample matrices.

Mantel test for association between species and environmental data matrices	
Standardized Mantel statistic (r)	0.147
Observed Z (sum of cross products)	0.209E+07
Average Z from randomized runs	0.204E+07
Variance of Z from randomized runs	0.389E+09
Minimum Z from randomized runs	0.197E+07
Maximum Z from randomized runs	0.211E+07
Number of runs with Z < observed Z	995
Total number of runs	1000
P-value =	0.006

$p = (1 + no.\ permutations >= observed)/(1 + no.\ permutations)$

The CCA (Canonical Correspondence Analysis) showed a strong relationship between environmental variables and fish CPUE by species across samples. The Monte Carlo test of significance for the ordination axes

resulted in highly significant p-values for the first three canonical axes, as well

as for the species-environment correlations (Table 2.9). Water chemistry

parameters, macrophyte coverage and habitat complexity accounted for 66.7

% of the catch distribution of the 76 fish species in the dataset (Table 2.10).

Table 2.9. Monte Carlo test of significance of the CCA first three canonical axes and species-environment correlations for fish assemblage structure at Marchantaria Island in the Amazon floodplain.

Monte Carlo test of significance of CCA canonical axis (number of permutations = 999)					
Eigenvalues			Permutations results		
Axis	Observed Eigenvalues	Mean	Minimum	Maximum	p
1	0.271	0.065	0.044	0.113	0.001
2	0.102	0.048	0.036	0.075	0.001
3	0.073	0.040	0.030	0.053	0.001
Species-environment correlations			Permutations results		
Axis	Observed Spp-Env. corr.	Mean	Minimum	Maximum	p
1	0.887	0.554	0.453	0.724	0.001
2	0.798	0.433	0.604	0.743	0.001
3	0.739	0.594	0.396	0.698	0.001

$p = (1 + no. \text{ permutations} >= observed)/(1 + no. \text{ permutations})$

The first environmental axis was strongly influenced by changes in

water transparency, electrical conductivity, water temperature and hydrogen

sulphide concentrations, which decreased along the axis, whereas water

depth and dissolved oxygen concentrations increased (Fig. 2.11). Water

transparency was positively correlated to water temperature and negatively

correlated to dissolved oxygen concentrations. Habitat complexity had a

significant positive correlation to water depth and vegetation coverage (Table

2.11). Aquatic macrophytes changed from murim with predominantly negative

scores along axis 1, to *Eichhornia*, *Pistia* and membeca with positive scores (Fig. 2.12). The first environmental axis reflects largely a gradient of water chemistry and turbidity changes from the interior of the floodplain towards the river channel. Negative scores on environmental axis 1(Fig. 2.13 Table 2.10) represent areas further from the river, the water is more transparent, warmer, has higher electrical conductivity, tends to be hypoxic and with noticeable concentrations of hydrogen sulphide (Fig. 2.13, Table 2.10, Table 2.11).

Table 2.10. Canonical correspondence analysis results for fish assemblage in the Amazon floodplain. (* statistically significant $P < 0.05$)

Variable	Canonical coefficients for environmental variables				Correlation of environmental Variables With species axes			
	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4
Water temperature	-0.15*	0.05	-0.20*	0.18	-.383*	.083	-.056	.059
Dissolved Oxygen	0.32*	-0.29*	0.42*	0.19	.598*	-.365*	.156	-.051
Depth	0.26*	0.60*	-0.14*	-0.25*	.495*	.503*	-.244*	-.046
Secchi	-0.38*	0.15	0.09	0.25	-.664*	.313*	-.131	.133
Hydrogen Sulphide	-0.14*	0.02	0.15	-0.00	-.254*	.046	.011	-.049
Electrical Cond.	-0.05	0.32*	0.57*	0.05	-.342*	.259*	.464*	.009
%vegetation cover	0.04	-0.11	-0.37*	0.40*	.239*	-.055	-.354*	.217*
%Membeca	0.11	0.31	-1.09*	-1.35*	.190*	.032	-.380*	.043
%Pistia	0.11	0.17	-0.23	0.14	.156	.213*	.237*	.408*
%Eichhornia	0.23*	0.43*	-0.23	-0.50*	.373*	.475*	.130	-.014
%Canarana	0.08	-0.10	-0.28	-0.63*	-.162	-.288*	.266*	-.334*
%Murim	0.02	-0.04	-0.45*	0.04	-.266*	-.005	-.168*	-.094
%Panicum	-0.01	-0.00	-0.50*	-0.17	-.168*	-.171*	-.031	.120
Habitat complexity	0.17	-0.30	0.48*	1.11*	.421*	.134	.216*	.335*

Summary statistics for ordination axes

	Axis 1	Axis 2	Axis 3	Axis 4
% of species-env. relation	35.7	49.2	58.9	66.7

Sum of all eigenvalues	3.848
Sum of all canonical eigenvalues	0.757
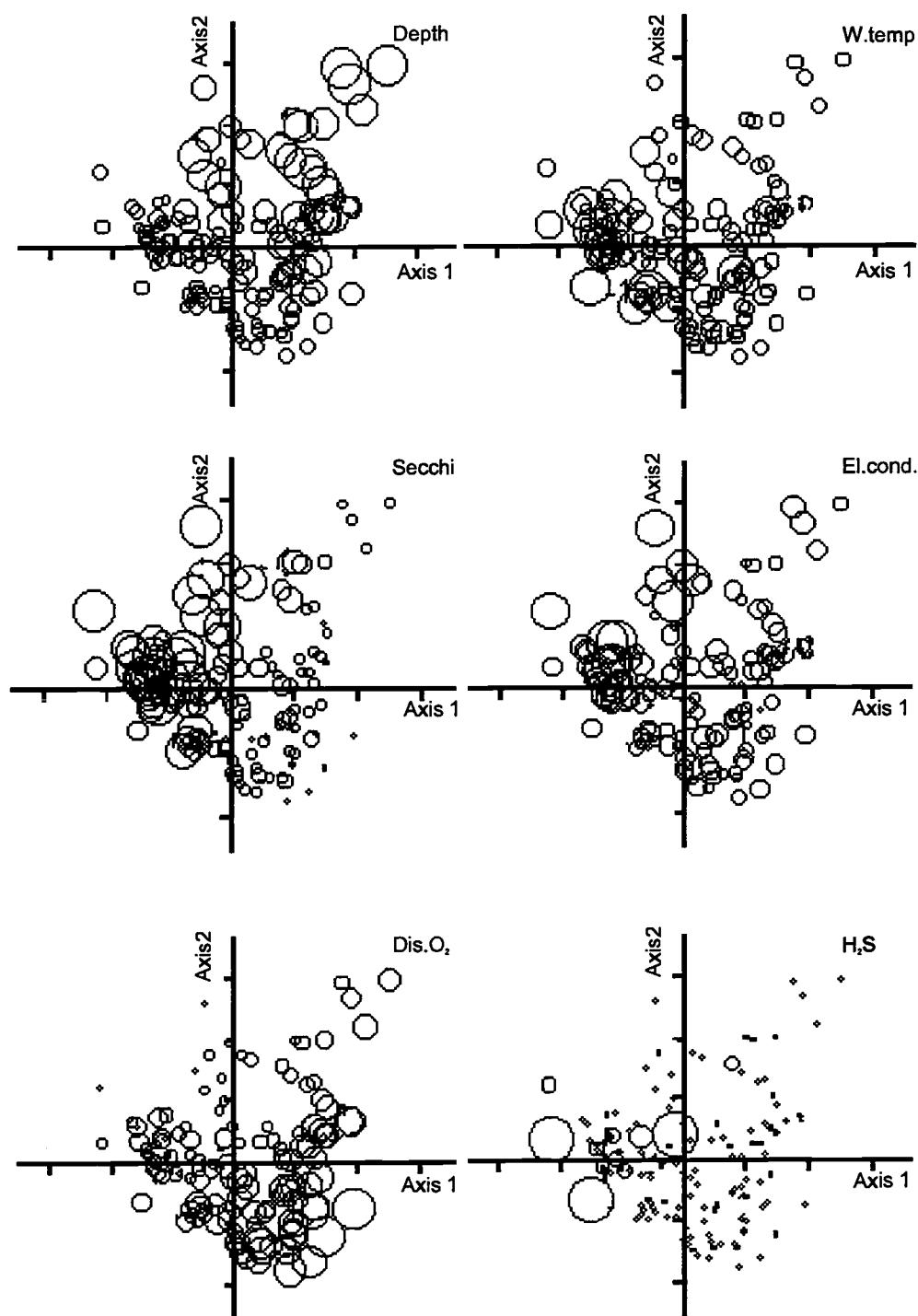
Figure 2.11. CCA scatterplots of water physico-chemical variables influences in defining the environmental gradients. Diameters of the circles are proportional to the parameter values.
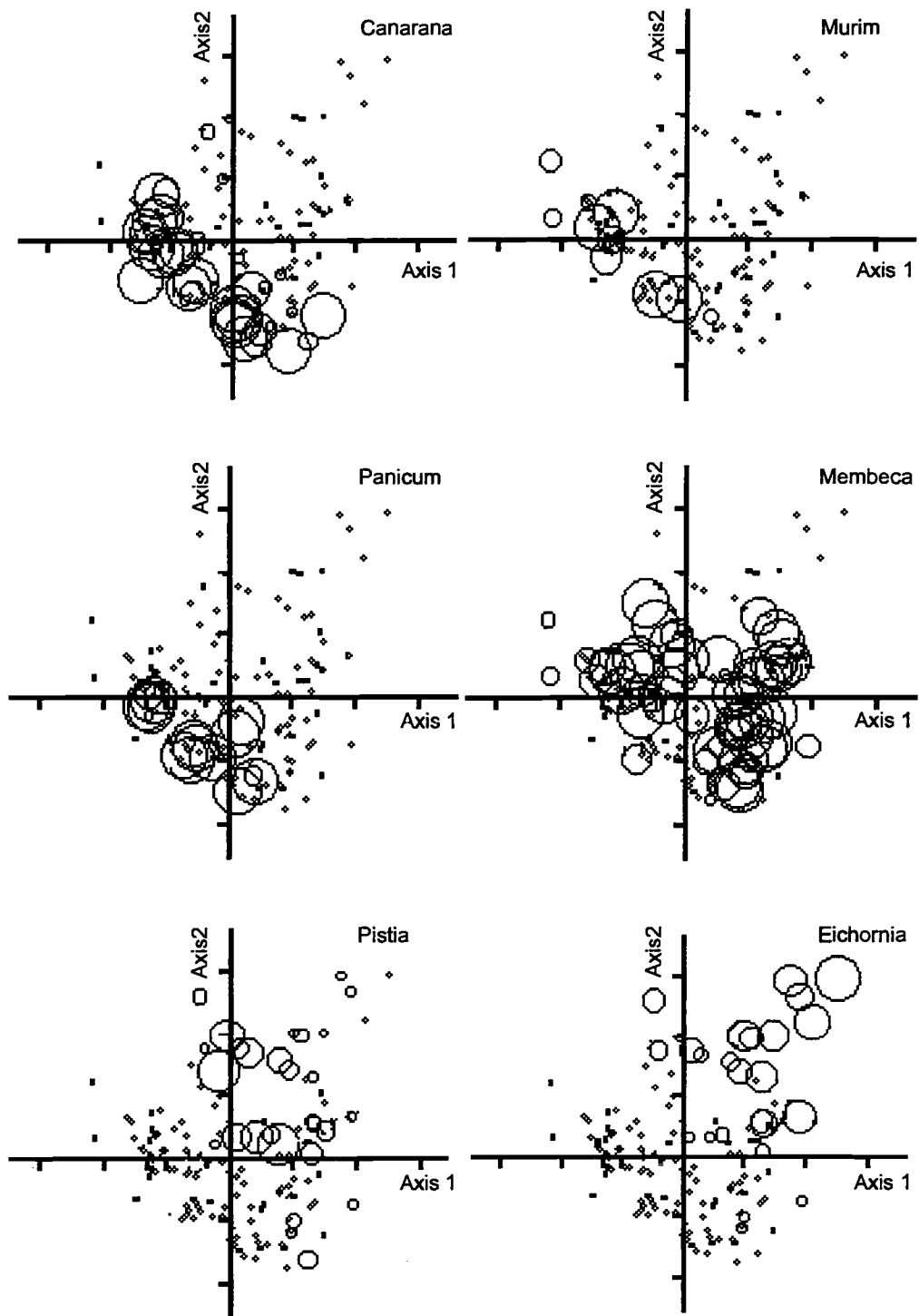
Figure 2.12. CCA scatterplots of aquatic macrophytes influences in defining the environmental gradients. Diameters of the circles are proportional to variable values.
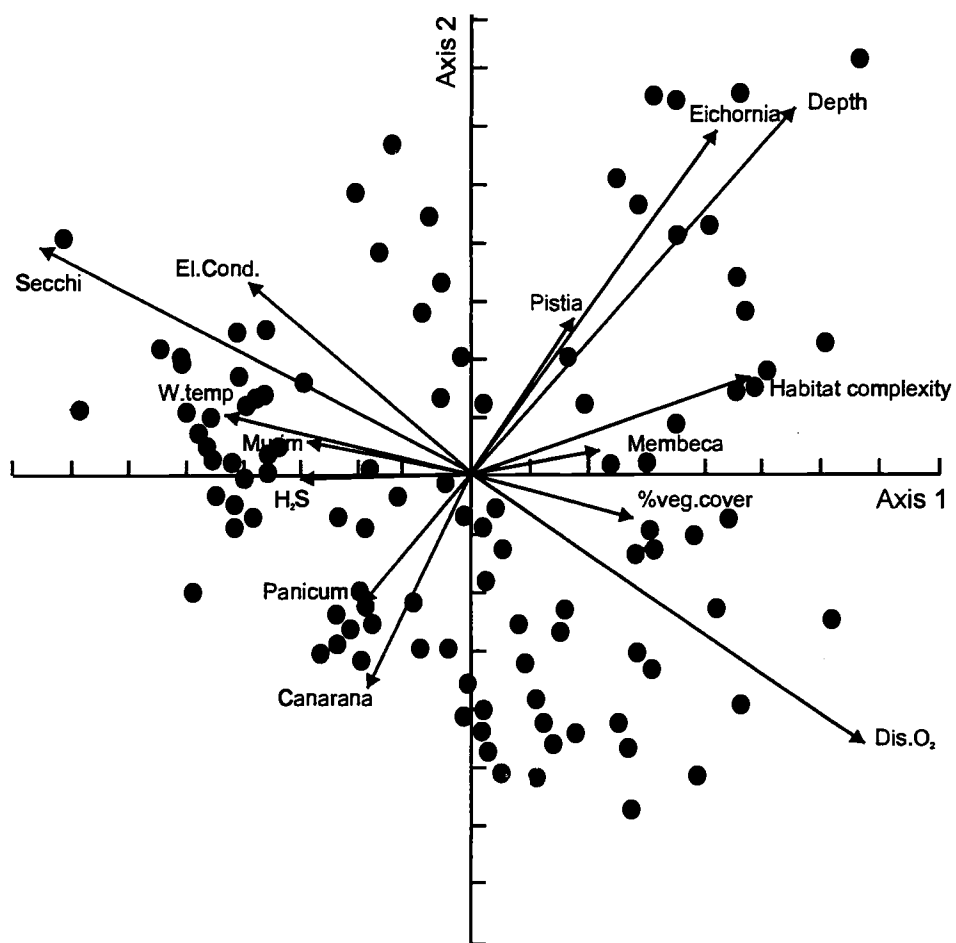
Figure 2.13. CCA joint plot of samples scores in relation to the canonical axes. Circles represent samples. Arrows indicate the environmental variables and their respective variation in relation to the canonical axes.

Closer to the river channel (positive scores on axis 1) the water is turbid, cooler, and well oxygenated. This axis also represent an aquatic macrophytes gradient associated with depth, in which shallow areas covered with murim change towards deeper areas covered with membeca (Fig. 2.11, 2.12 and 2.13, Table 2.11). The second axis is dominated by depth and macrophyte composition. The gradient changes from shallow areas where the rooted grasses canarana and *Panicum* predominate (negative scores on axis 2), to deeper areas with the free floating macrophytes *Eichhornia* and *Pistia* (positive scores on axis 2) (Fig. 2.13, Table 2.10, Table 2.11).

Fish species grouped by trophic guilds showed that omnivores had ubiquitous distribution along axis 1, whereas detritivores and piscivores did not (Fig.2.14, Table 2.12). Detritivores species such as *Psectrogaster rutiloides, Potamorhina latior, Semaprochilodus insignis, Semaprochilodus taeniurus,* had negative scores on the first axis (Table 2.12, Fig. 2.15). Piscivores, omnivores, planktivores, scale eaters and insectivores had positive axis 1 scores (Table 2.12). Piscivores could be further separated into two groups based on scores along axis 2 (Fig. 2.14, Table 2.12). One group of 10 species with positive scores along axis 2 was most frequently caught in moderate to low turbidity. This group was dominated by the clupeids *Pellona castelnaeana, P. flavipinnis*, the piranhas *Pygocentrus nattereri, Serrasalmus rhombeus* and *S. spilopleura*, as well as the auchenipterid catfishes *Auchenipterus nuchalis* and *Parauchenipterus galeatus*.

Table 2.11. Canonical correspondence analysis Pearson correlation coefficients matrix of species axes, environmental axes and environmental variables. These Correlations are the coordinates of the arrowhead for each environmental variable along each canonical axis shown in the CCA biplots. Environmental variables are: water temperature (WT°C), dissolved oxygen (DO), water depth (Depth), water transparency (Secchi), Hydrogen sulphide (H2S), electric conductivity (EC), percent vegetation cover (%Veg), percent membeca (%MEM), percent Pistia (%PIS), percent *Eichhornia* (%EIC), percent canarana (%CAN), percent murim (%MUR), percent *Panicum* (%PAN), and habitat complexity (HC). SP-AX and ENV-AX stand for species axis and environmental axis respectively.

	SP AX1	SP AX2	SP AX3	ENV AX1	ENV AX2	ENV AX3	WT°C	DO	Depth	Secchi	H2S I	EC	%Veg	%MEM	%PIS	%EIC	%CAN	%MUR	%PAN
SP AX1	1																		
SP AX2	-0.032	1																	
SP AX3	0.080	-0.011	1																
ENV AX1	0.887	0.000	0.000	1															
ENV AX2	0.000	0.798	0.000	0.000	1														
ENV AX3	0.000	0.000	0.739	0.000	0.000	1													
WT°C	-0.384	0.084	-0.056	-0.433	0.105	-0.076	1												
DO	0.598	-0.366	0.157	0.675	-0.458	0.212	-0.049	1											
Depth	0.495	0.503	-0.245	0.558	0.630	-0.331	-0.102	0.071	1										
Secchi	-0.664	0.313	-0.132	-0.749	0.393	-0.178	0.357	-0.686	-0.077	1									
H2S	-0.255	0.047	0.012	-0.288	0.058	0.016	0.227	-0.083	-0.023	0.103	1								
EC	-0.343	0.259	0.464	-0.386	0.325	0.628	0.212	-0.244	-0.304	0.261	0.015	1							
%Veg	0.239	-0.055	-0.355	0.271	-0.069	-0.480	-0.084	0.075	0.238	0.006	-0.016	-0.252	1						
%MEM	0.190	0.033	-0.380	0.214	0.041	-0.514	0.121	0.108	0.368	0.076	-0.004	-0.225	0.427	1					
%PIS	0.156	0.213	0.237	0.176	0.267	0.321	-0.186	-0.055	0.029	-0.047	-0.058	0.225	0.016	-0.286	1				
%EIC	0.373	0.475	0.131	0.422	0.596	0.177	-0.137	0.016	0.415	-0.129	-0.066	-0.002	-0.019	-0.308	0.247	1			
%CAN	-0.162	-0.288	0.267	-0.183	-0.361	0.361	0.125	0.083	-0.384	-0.081	0.052	0.202	-0.028	-0.444	-0.150	-0.160	1		
%MUR	-0.266	-0.006	-0.169	-0.300	-0.007	-0.228	-0.041	-0.216	-0.190	0.096	0.167	0.020	-0.291	-0.211	-0.087	-0.087	-0.121	1	
%PAN	-0.169	-0.171	-0.031	-0.191	-0.214	-0.042	0.046	-0.008	-0.198	-0.002	-0.067	-0.083	-0.272	-0.323	-0.112	-0.113	-0.169	-0.064	1
HC	0.421	0.134	-0.217	0.476	0.168	-0.293	-0.038	0.128	0.506	-0.040	-0.121	-0.270	0.437	0.755	0.090	0.071	-0.548	-0.438	-0.159

Table 2.12. Canonical Correspondence Analysis ordination scores for the 76 fish species. Trophic Guilds: (D) detritivores, (I) Insectivores, (L) Lepidivores, (O) Omnivores, (P) Piscivores and (K) Planktivores.

Species	Species acronym	Axis 1 scores	Axis 2 scores	Axis 3 scores	Axis 4 scores	Species Weight
Ageneiosus dentatus (P)	AGEDE	1.5168	0.782	0.3452	-0.721	9.41
Auchenipterus nuchalis (P)	AUCNU	1.3469	1.2874	-0.2357	-0.5579	12.08
Apteronotus sp (I)	APTsp	1.1984	0.5129	0.2471	0.6288	12.26
Centromochlus heckelii (O)	CENHE	1.1175	0.8807	0.3604	-0.7589	18.24
Hypophthalmus marginatus (K)	HYPMA	1.1156	0.5872	-0.1346	-0.5044	17.54
Pristigaster cayana (P)	PRICA	1.0306	-0.0521	0.3539	0.023	10.23
Pellona castelnaeana (P)	PELCA	1.0045	0.3491	0.4024	0.1357	23.42
Trachidoras sp (O)	TRAsp	0.9968	0.5963	-0.3459	-0.1755	14.45
Anchovia surinamensis (K)	ANCSU	0.9427	0.4211	0.2909	0.399	16.87
Rhaphiodon vulpinus (P)	RHAVU	0.9162	-0.0361	0.1141	-0.1391	91.65
Apteronotus hasemani (I)	APTHA	0.8994	-0.1104	-0.5777	-0.0074	7.11
Apteronotus bonaparti (I)	APTBO	0.8637	0.448	0.221	-0.2779	6.62
Charax hemigrammus (O)	CHAHE	0.8372	-0.032	0.1846	-0.2055	25.2
Pellona flavipinnis (P)	PELFL	0.8231	0.2853	0.4139	0.2444	13.03
Sorubim lima (P)	SURLI	0.7807	-0.584	-0.234	-0.308	21.05
Pimelodus blochi (P)	PIMBL	0.7278	-0.3413	0.0007	0.0953	106.4
Parauchenipterus galeatus (P)	PARGA	0.7068	0.9906	0.4513	0.5226	12.33
Roeboides meyeri (L)	ROEME	0.6601	-0.843	0.6388	0.1209	8.56
Colomesus psitacus (I)	COLPS	0.6425	-0.6022	-0.1748	0.1434	9.64
Agoniates anchovia (P)	AGOAN	0.6245	-0.0037	0.3495	-0.649	5.7
Hyphessobrycon calisticus (O)	HYPCA	0.5688	0.5075	0.2294	-0.2868	78.93
Serrasalmus rhombeus (P)	SERRH	0.56	0.1266	-0.1611	-0.1525	89.8
Lycengraulis batesi (O)	LYCBA	0.5413	-1.0279	1.2164	-1.4471	6.24
Brycon melanopterum (O)	BRYME	-1.0226	0.2487	0.2002	0.5407	11.59
Semaprchilodus insignis (D)	SEMIN	-1.0149	0.1878	-0.1233	-0.0556	113.48
Brycon erythropterus (O)	BRYER	-0.97	0.3631	0.4671	0.38	57.29
Psectrogaster rutiloides (D)	PSERU	-0.9338	0.3449	-0.51	-0.0942	47.43
Psectrogaster sp (D)	PSTsp	-0.9144	-0.018	0.0448	-0.2635	105.92
Potamorhina sp (D)	POTsp	-0.8084	0.3773	-0.4951	-0.017	45.82
Hoplosternum thoracatum (D)	HOPTH	-0.8053	0.0967	-0.3532	-0.2748	11.92
Astronotus ocelatus (O)	ASTOC	-0.6872	0.2251	-0.0205	0.4685	9.78
Prochilodus nigricans (D)	PRONI	-0.6793	0.1132	-0.1071	-0.1563	31.17
Eigenmanina melanopogon (O)	EIGME	-0.6492	0.0975	0.8332	0.2168	41.47
Piaractus brachipomus (O)	PIABR	-0.6348	-0.2032	0.1184	0.4881	41.69
Potamorhina latior (D)	POTLA	-0.6344	-0.2151	-0.0184	0.1554	28.68
Hoplosternum litoralli (D)	HOPLI	-0.5707	0.3658	-0.9179	-0.2818	6.33
Semaprochilodus taeniurus (D)	SEMTA	-0.5698	-0.1341	-0.2074	-0.1714	96.81
Triportheus angulatus (O)	TRIAN	-0.5453	0.0066	0.1154	-0.2639	68.77
Triportheus elongatus (O)	TRIEL	-0.5074	0.046	0.1945	-0.0778	159.96
Colossoma macropomum (O)	COLMA	-0.5051	0.1177	0.2781	0.7204	22.25
Serrasalmus spiropleura (P)	SERSP	0.4558	0.5353	-0.1589	0.4924	32.57
Aphyocharax alburnus (O)	APHAL	0.4492	-0.4749	-0.0867	-0.0423	93.48
Rhythiodus microlepis (O)	RHYMI	0.448	-0.3805	-0.4042	-0.1661	57.91
Hemigrammus bellottii (O)	HEMBE	0.4339	-1.0177	-0.1027	-0.545	10.97

Table 2.12. Continued

Species	Species acronym	Axis 1 scores	Axis 2 scores	Axis 3 scores	Axis 4 scores	Species Weight
Roeboides thurni (L)	ROETH	0.4327	-0.526	-0.2693	0.306	72.4
Synbranchus marmoratus (P)	SYNMA	0.4257	1.2611	0.2289	0.1163	40.56
Hydrolicus scomberoides (P)	HYDSC	0.4146	-0.4894	0.0992	0.2494	13.46
Mylossoma duriventri (O)	MYLDU	0.373	0.0952	-0.1502	0.1632	238.25
Charax stenopterus (L)	CHAST	0.345	-0.6173	-0.3051	0.2495	8.18
Pseudoplatistoma sp1 (P)	PSEsp	0.3132	-0.2432	0.0942	0.3077	17.23
Hypoptopoma gulare (D)	HYPGU	0.2794	-1.0151	0.3009	-0.2149	30.61
Hoplias malabaricus (P)	HOPMA	0.2675	0.2627	-0.1007	-0.0673	82.02
Leporinus friderici (O)	LEPFR	0.2167	-0.3268	0.2989	0.4843	50.37
Laemonita proximus (O)	LAEPR	0.2072	-0.0136	-0.4976	-0.0752	31.48
Mylossoma aureum (O)	MYLAU	0.1591	-0.0799	0.0154	0.1277	337.72
Pygocentrus nattereri (P)	PYGNA	0.1523	0.0516	-0.1015	0.2269	139.79
Schizodon fasciatus (O)	SCHFA	0.1419	-0.1346	0.2914	0.3144	110.76
Cheirodon piaba (O)	CHEPI	0.1326	0.2856	-0.0179	-0.2072	147.72
Eucynopotamus biserialis (O)	EUCBI	0.0877	-0.117	0.0705	-0.3306	16.82
Acarichthys heckelii (O)	ACAHE	0.0862	-0.8886	0.5517	-0.3876	33.38
Cichla monoculus (P)	CICMO	0.0502	-0.3643	0.1905	-0.1114	10.61
Cordoras hastatus (D)	CORHA	0.0015	-0.3255	-0.5787	0.0847	38.29
Hyphessobrycon sp4 (O)	HYPsp4	-0.0215	-0.0252	-0.8384	0.2024	33.89
Odontostilbe fugitiva (O)	ODOFU	-0.026	-0.3072	0.3066	-0.2646	51.35
Moenkhausia intermedia (O)	MOEIN	-0.0328	-0.0824	-0.0232	-0.0499	185.59
Cichlasoma Amazonarum (O)	CICAM	-0.0584	0.1617	-0.1261	-0.0392	162.35
Pyrrhulina sp (O)	PYRsp	-0.0742	0.2068	-0.783	-0.1532	7.62
Satanoperca jurupari (O)	SATJU	-0.1236	-0.7059	0.5637	-1.2731	9.94
Chaetobranchopsis orbicularis (K)	CHAOR	-0.1758	0.3088	-0.5466	0.0567	8.99
Laemonita taeniata (O)	LAETA	-0.2065	-0.0443	-0.353	-0.0748	91.31
Hyphessobrycon sp2 (O)	HYPsp2	-0.2544	0.2721	0.9776	0.0333	38.98
Ctenobrycon hauxwellianus (O)	CTEHA	-0.3095	-0.0118	-0.0917	-0.0237	272.82
Psectrogaster Amazonica (D)	PSEAM	-0.3181	0.0524	0.1693	0.4839	27.74
Liposarcus pardalis (D)	LIPPA	-0.4287	-0.2562	0.1254	0.0217	158.53
Mesonauta insignis (O)	MESIN	-0.4499	-0.2704	0.5416	0.2095	8.49
Moenkhausia lepidura (O)	MOELE	-0.4853	0.0957	0.3402	-0.6041	46.76

Eight piscivore species with negative scores along axis 2 were most frequently caught in high turbidity and moderate to high dissolved oxygen. This group was dominated by Hydrolicus scomberoides, Rhaphiodon vulpinus, Cichla monoculus, and the pimelodid catfishes Pimelodus blochi and Sorubim lima.

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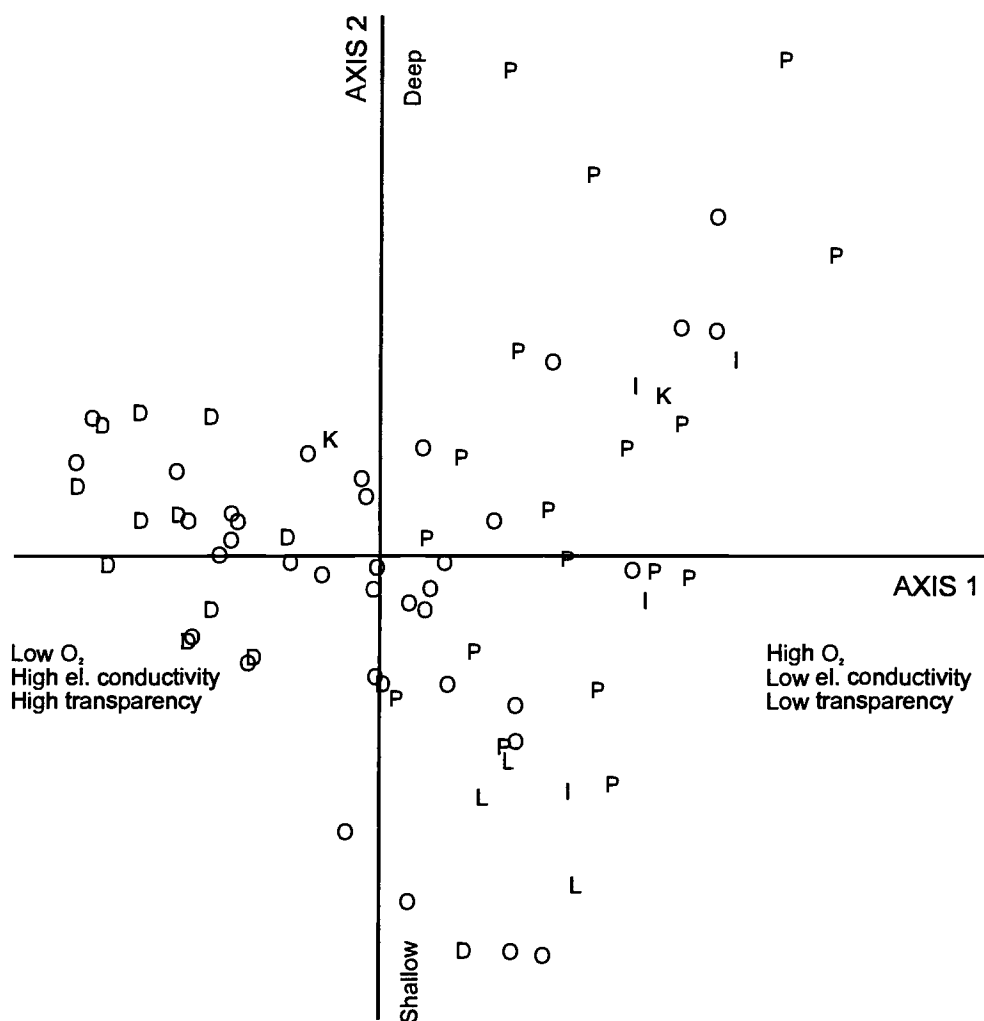
Figure 2.14. CCA ordination biplot showing fish species distribution in relation to the first two ordination axes by trophic guilds. Species positions along gradients are represented by their centroids based on $\log_e(CPUE+1)$ for each sample, and plotted by trophic guilds: (D) detritivores, (I) insectivores, (K) planktivores, (L) lepidivores, (O) omnivores and (P) piscivores.

Species scores along the environmental axes formed a cluster of species centroids aligned in a 45 degree angle in relation to the first canonical axis and follows the orientation of the water turbidity and dissolved oxygen gradient (Fig. 2.15). An assemblage of 17 species of curimatids, prochilodontids and characids with negative scores on axis 1 dominated areas deeper in the floodplain (sampling areas A4 and A5, Fig.2.1). Despite the poor environmental conditions in which these fish occurred, this assemblage accounted for 35.5% of the total catch across all samples. The catch distribution pattern of a subset of these species is shown in Fig. 2.16. Only three of the thirty-one species of catfishes were part of this assemblage, two callichthyiids and one loricariid.

A group of 13 species with positive scores on axis 1 characterized a second assemblage on the other extreme of the gradient where water is cooler, turbid and rich in dissolved oxygen. The pelagic predators *Pellona*, *Rhaphiodon* and *Hydrolicus*, as well as pimelodid catfishes and gymnotiforms composed this assemblage. This assemblage only accounted for 3.5% of the total catch, but their relatively high scores along the ordination axes and their distribution pattern made them an important group in determining the overall structure of the fish community in the Amazon floodplain (Fig. 2.17, Table 2.12). A smaller cluster of species formed by auchinepterid, ageneiosid and hypophthalmid catfishes as well as the synbranchid eel formed a separate assemblage that tended to dominate in areas with deeper water covered by patches of *Eichhornia crassipes*.
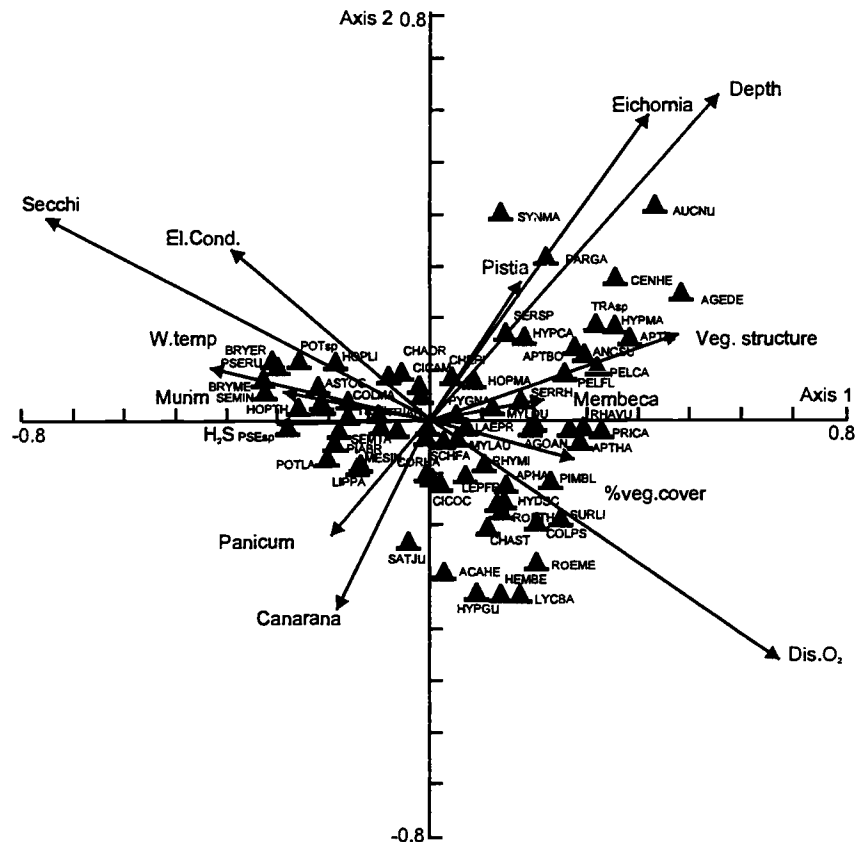
Figure 2.15. CCA joint plot of species distribution in relation to the environmental axes. Species are represented by their centriods based on $\log_e(CPUE+1)$ for each sample. Arrows indicate the environmental variables and their respective variation in relation to the canonical axes; species acronyms are given in table 2.12.

Cichlids and smaller tetragonopterin characids formed a cluster of species that tended to dominate shallow, well-oxygenated areas covered by *Echinochloa* and *Panicum*.

The most abundant species such *as Mylossoma aureum*, *Pygocentrus nattereri*, *Cichlassoma Amazonarum*, *Hoplias malabaricus* and *Liposarcus pardalis*, had heavy weight in determining the species ordination axes.
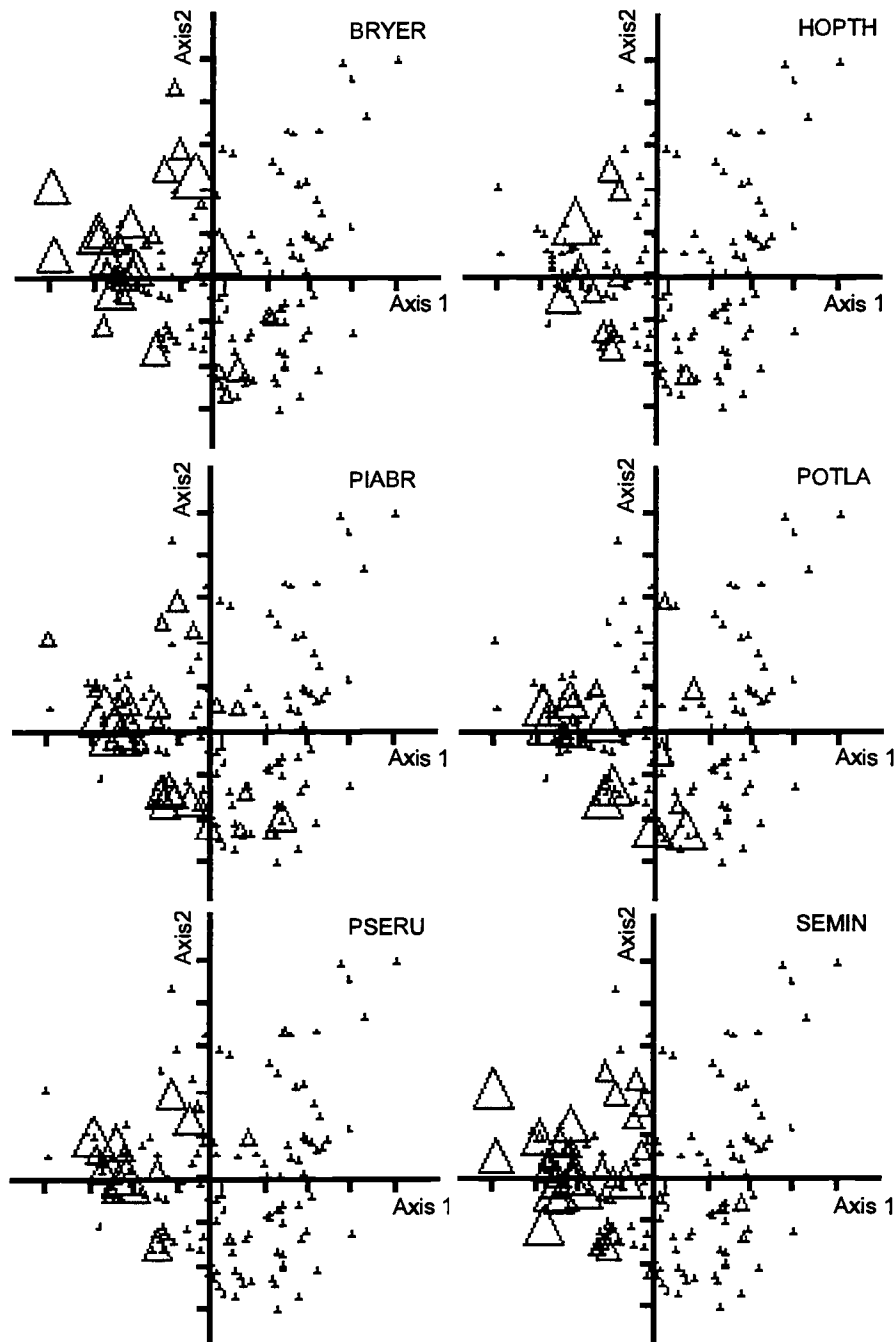
Figure 2.16. CCA scatterplots of fish species distribution along the canonical axes, group of fish that occur mostly in hypoxic habitats. Triangles sizes are proportional to species catch per sample (log_e(CPUE+1)). BRYER (*Brycon erithropterus*), HOPTH (*Hoplosternum thoracatum*), PIABR (*Piaractus brachipomus*), POTLA (*Potamorhina latior*), PSERU (*Psectrogaster rutiloides*) and SEMIN (*Semaprochilodus insignis*).
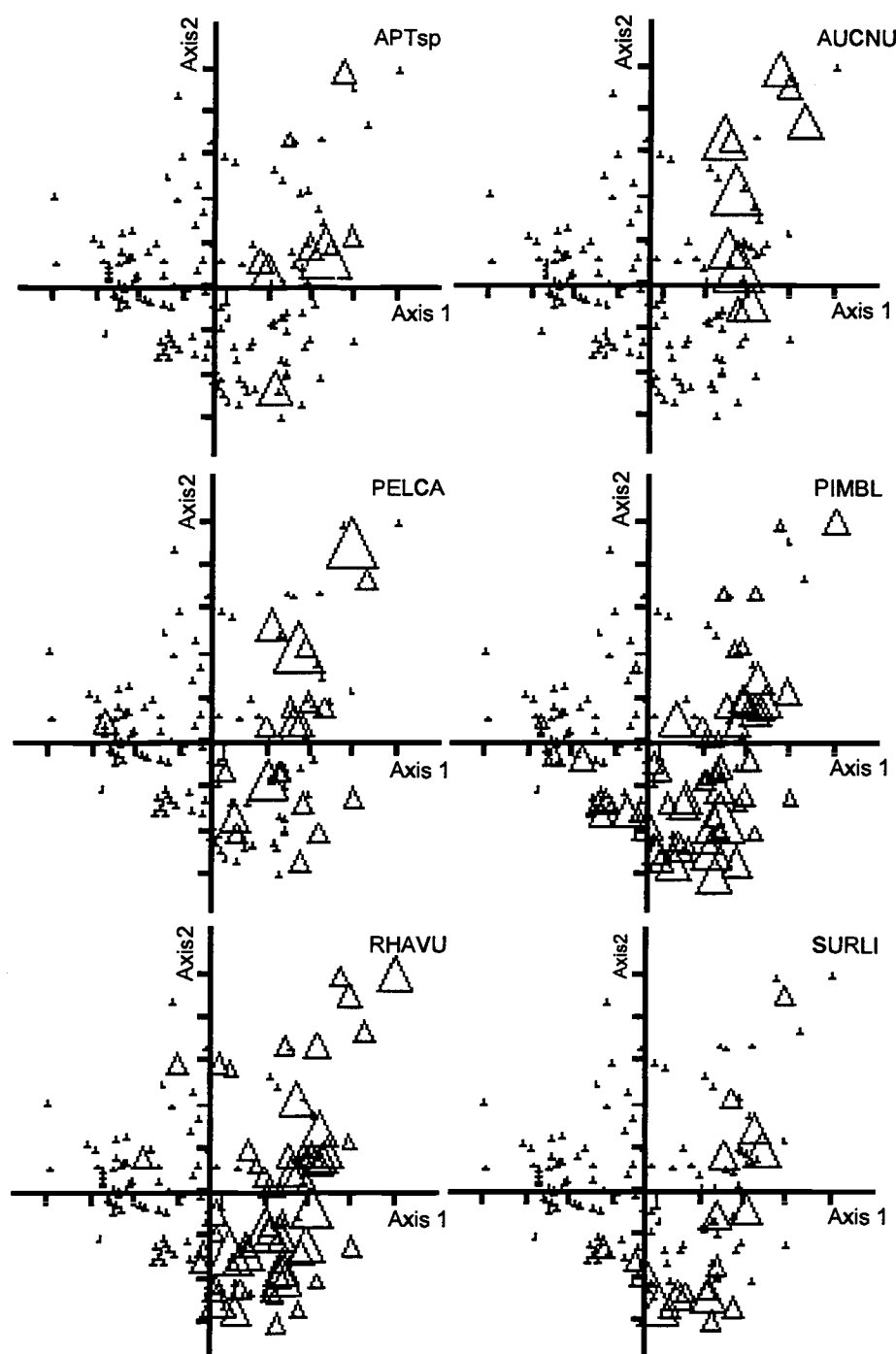
Figure 2.17. CCA scatterplots of fish species distribution along the canonical axes, group of fish that occur mostly in turbid water with high oxygen. Triangle's sizes are proportional to species catch per sample ($\log_e$(CPUE+1)). APTsp (*Apteronotus sp*), AUCNU (*Auchenipterus nuchalis*), PELCA (*Pellona castelnaeana*), PIMBL (*Pimelodus blochi*), RHAVU (*Rhaphiodon vulpinus*) and SURLI (*Sorubim lima*).

However, their low canonical scores on all axes and their ubiquitous

distribution undermined their importance to define species assemblage

characteristics (Fig. 2.18, Table 2.12).
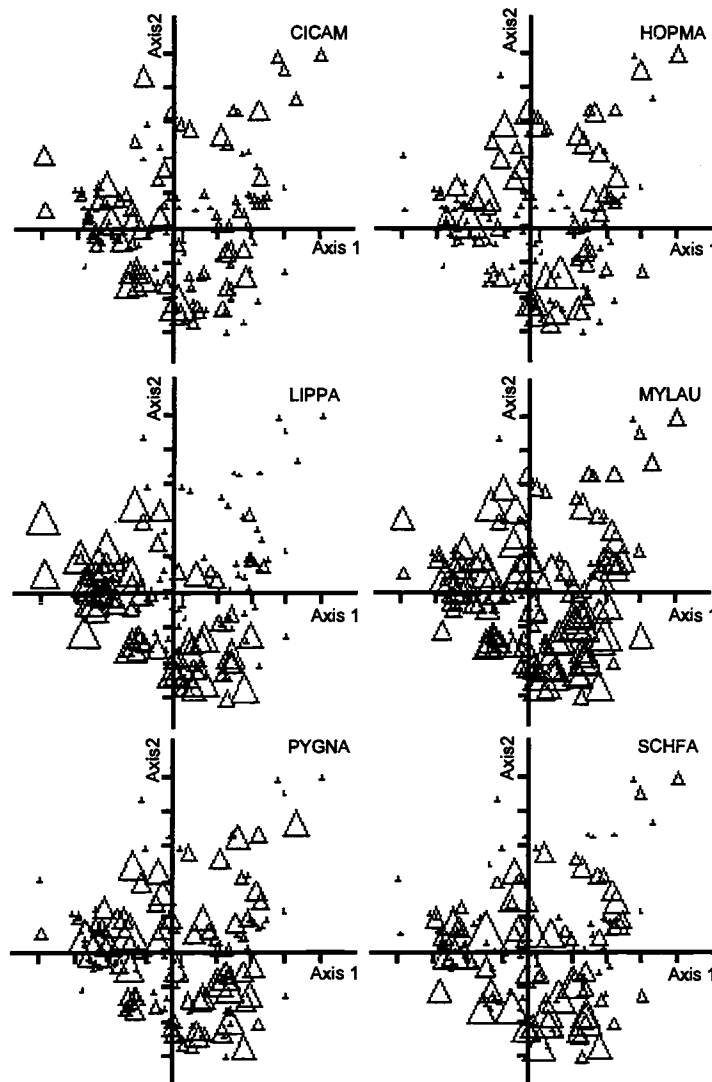
Figure 2.18. CCA scatter plots of fish species distribution along the canonical axes, group of fish that occur across all habitats. Triangles sizes are proportional to species catch per sample ($\log_e$(CPUE+1)). CICAM (*Cichlassoma amazonarum*), HOPMA (*Hoplias malabaricus*), LIPPA (*Liposarcus pardalis*), MYLAU (*Mylossoma aureum*), PYGNA (Pygocentrus nattereri) and SCHFA (Schizodon fasciatus).

Indicator species analysis

Indicator species analysis revealed that the majority of the 76 species had ubiquitous distributions in relation to macrophytes; nevertheless 26.3% (20 species) had strong affinity for a particular macrophyte type (Table 2.13). Similarly, 25% (19 species) showed distribution affinity to particular dissolved oxygen conditions (Table 2.14). Eight detritivore species had significant indicator values for the murim strata (Table 2.13), whereas none of the other trophic guilds had any strong affinity for any particular strata. Similar to the CCA results, *Synbranchus marmoratus* and the auchenipterid catfishes *Auchenipterus nuchalis* and *Parauchenipterus galeatus* had significant indicator value for *Eichhornia* patches. Six detritivores had significant indicator values for hypoxic conditions, whereas piscivores limited their distribution almost exclusively in areas where oxygen concentrations were above 1mg/l (Table 2.14).

Table 2.13. Indicator species analysis using vegetation types to group samples. EIC (*Eichhornia*), CAN (Canarana), MEM (Membeca), MUR (Murim), PAN (*Panicum*), PIS (*Pistia*) and UNV (Unvegetated). Table shows only species with significant indicator value. (* proportion of randomized trials with indicator value equal to or exceeding the observed indicator value. Guilds: (D) detritivores, (O) Omnivores and (P) Piscivores.

Indicator values % of perfect indication for each class. group							Observed	Monte Carlo sign. test Rand. permutations		
Species (Guild)	UNV	CAN	EIC	MEM	PIS	PAN	MUR	IV	AVE	S.dev.	P*
LIPPA (D)	0	17	0	5	8	13	28	28.3	14	3.08	0.002
SEMIN (D)	0	5	0	4	0	12	27	26.9	11.4	3.69	0.004
POTsp (D)	0	1	1	3	0	1	26	26.1	8.7	4.04	0.003

Table 2.13. Continued

TRIAN (O)	2	10	0	5	3	1	26	25.6	11.5	3.64	0.004
PRONI (D)	0	2	0	3	0	2	24	23.8	8.9	3.92	0.008
PSTsp (D)	0	7	0	2	0	7	24	23.8	9.8	3.84	0.007
HOPLI (D)	0	0	0	1	0	2	13	12.8	5.8	3.43	0.049
MYLAU (O)	2	12	9	22	19	17	10	22.3	16.6	1.43	0
CHEPI (O)	0	8	12	20	2	0	8	19.8	13.3	3.25	0.041
PIABR (O)	0	2	0	1	3	22	6	21.7	9.6	4.13	0.017
MYLDU (O)	0	7	18	23	19	5	5	23.5	15.8	2.35	0.004
MOELE (O)	22	2	2	2	0	1	3	22.2	9.1	3.84	0.01
PYGNA (P)	0	7	4	23	18	6	1	23.1	14.3	3.11	0.017
SCHFA (O)	0	8	2	14	23	7	1	23.3	13.1	3.23	0.008
SERSP (P)	0	0	7	4	26	1	0	26.1	9.1	3.63	0.002
HYPGU (D)	0	19	0	3	0	13	0	19.4	9	3.87	0.019
HYPCA (O)	0	4	31	4	2	0	0	31.3	10.7	3.82	0
SYNMA (P)	0	0	32	5	9	0	0	31.7	9.5	3.66	0
PARGA (P)	0	0	18	1	11	0	0	17.8	6.9	3.93	0.023
AUCNU (P)	0	0	25	2	0	0	0	24.9	6.5	3.65	0.002

Table 2.14. Indicator species analysis using dissolved oxygen levels to group samples; hypoxic ($\leq$ 1ppm), intermediate (>1 $\leq$ 2 ppm) and oxygenated (> 2 ppm). Table shows only species with significant indicator values. (*indicator values equal or exceeding the observed indicator value). Guilds: (D) detritivores, (K) planktivores, (O) Omnivores and (P) Piscivores.

	Indicator values % of perfect indication for each classification group			Monte Carlo sign. test			
				Observed	Random. permutations		
Species (Guild)	Oxygenated	Intermediate	Hypoxic	(IV)	Mean	S.Dev	p*
SEMIN (D)	1	11	41	40.6	15.2	3.18	0
LIPPA (D)	10	18	33	32.6	22.6	3.36	0.012
PSERU (D)	0	1	28	27.6	8.3	3.16	0
POTsp (D)	0	5	26	25.6	9.3	2.94	0
BRYER (O)	1	11	24	23.5	11.9	3.07	0.002
SEMTA (D)	7	6	24	24.2	15.8	3.45	0.026
PSTsp (D)	2	9	18	17.8	11.6	3.14	0.042
COLMA (O)	1	3	16	15.6	8.1	2.85	0.024
RHYMI (O)	25	1	4	25	14.6	3.46	0.011
EIGME (O)	2	19	3	19	9.7	3.02	0.012
APHAL (O)	35	4	3	34.8	18.5	3.6	0
BRYME (O)	0	12	2	12	4.9	2.27	0.015
PIMBL (P)	37	8	2	36.6	19.8	3.53	0.002
CHAOR (K)	0	13	1	12.7	5.8	2.5	0.021
PRICA (P)	11	0	0	11.1	5.4	2.32	0.033
RHAVU (P)	47	5	0	47.3	19.6	3.67	0
PELCA (P)	16	2	0	16.4	9.7	3.13	0.038
AGEDE (P)	12	0	0	12.3	5.7	2.46	0.022
SURLI (P)	15	2	0	15.2	8.8	2.99	0.04

Discussion

Taxonomic composition

Gear efficiency in detecting species richness present in the study area was less than 100 percent and detectability varied according to catchability and numbers of each species present. Independent estimations of species richness based on extrapolation using first and second order jackknife estimators (Palmer, 1990; Palmer, 1991) suggests that the estimated total species richness for Marchantaria Island is higher than the numbers obtained by my sampling (Table 2.2). Nevertheless, because of the high proportion of species with only one and two occurrences in the data set (26%), and the known sensitivity of these estimators to the presence of rare species (Palmer, 1995), the expected number of species may be overestimated by some degree. However, Comparing my results with prior studies (Bayley, 1983; Junk et al., 1983) showed that four families (Potamotrygonids, Osteoglossids, Belonids and Soleids) known to occur at Marchantaria Island were not captured during this study. The absence of these taxa was likely an effect related to the types of habitats that I sampled, rather than gear efficiency, although (Bayley and Herendeen, in press) showed that diverse benthic demersal fishes such as doradids, loricariids, pimelodids, and Gymnotiforms had lower catchability than pelagic schooling species and shelter seeking species. For example, (Bayley, 1983) noted that although *Osteoglossum bicirrhosum* was commonly found in the study area, it was poorly represented

in his samples because of its ability to detect the approach of the sampling gear. Bayley and Herendeen, in (press) did find much lower catchability for the deep water method (A), but they did not find an effect in the gear catchability due to differences in environmental conditions nor vegetation structure of the sampling sites.

The comparison of cumulative ratios of fish species richness between my study and (Bayley, 1983) showed no differences. The results suggest that the gear was operated with similar performance to detect the diversity of fishes present in Marchantaria Island in both studies (Fig. 2.6a). The difference in total number of species detected was likely an effect of sampling effort and/or inter-annual differences (Merona and Bittencourt, 1993).

The taxonomic composition of my data set was similar to prior studies conducted at Marchantaria Island. Characiformes were dominant in my study (45%) as well as in (Bayley, 1983) (41%) and (Junk et al., 1983) (37%). Gymnotiformes had 16% in terms of species numbers versus 7% and 10% (Bayley, 1983) and (Junk et al., 1983) respectively. Siluriformes and Perciformes were less represented in my study when compared to the same studies. These differences could be related to the sampling design differences and potentially to inter-annual variability. Also, in all three studies the percentage of rare species with one and two occurrences was high, ranging from 26% of the species in the current study to 40% in Junk et al 1983, indicating that rarity is a common feature at the scale of the sampled quadrate. Rodriguez and Lewis, (1997) found a similar pattern for the Orinoco

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floodplain using boat electrofisher, where 21% of the species collected in their study were present only in one or two samples. This high percentage of rare species could also have influenced the differences in species richness estimates, because variability in detectability becomes more critical.

Effect of Habitat on fish distribution

All vegetated strata were found to have consistently higher fish species richness than the unvegetated habitats (Fig. 2.7). The same pattern was also found for other central Amazonian floodplain lakes (Fig. 2.8). My results show that species richness was associated with underwater architectural complexity of macrophytes, as shown by the species rarefaction curves. In this analysis, membeca and *Eichhornia* stands, with their dense and complex root system, hosted a greater number of species than other macrophytes (Fig. 2.6b). In similar studies in Wisconsin lakes, spatially complex habitats had a greater variety of microhabitats and supported a more diverse (Tonn and Magnuson, 1982; Eadie and Keast, 1984; Dibble et al., 1996; Weaver et al., 1997). Substrate diversity and vegetation complexity were the best predictors of fish species diversity in southern Ontario lakes (Eadie and Keast, 1984). (Weaver et al., 1997) suggested that structural patchiness instead of floristic composition was more important in explaining fish distribution. By providing spatial complexity, macrophyte patches may promote community stability by providing habitat heterogeneity (Stenseth, 1980)

All 139 species captured during this study were collected associated with macrophytes (Table 2.1), supporting the hypothesis that presence of habitat structural features might be the main factor in habitat usage by floodplain fishes. Strong associations of fishes to macrophytes were also reported for Lake Mamirauá in the Japurá river floodplain (Henderson and Hamilton, 1995; Henderson and Robertson, 1999), as well as for blackwater floating meadows in the Rio Negro (Araujo-Lima et al., 1986). Nonetheless, (Bonetto et al., 1969) and (Cordiviola, 1992) did not find the same degree of association between macrophytes and fishes in the lower Paraná basin. Only 57 % of species in their studies were found to be associated with macrophytes, despite the fact that the same macrophytes were present and that the fish fauna is relatively similar to the Amazon. This suggests that factors other than the presence of physical structure might be influencing habitat use in neotropical floodplains, and that sampling technique may be influential.

Although structural characteristics are an important aspect of habitat selection by fishes, biotic interactions might play a moderating role in defining associations between fishes and aquatic plants. Predators or facultative predators represented 39% of the total number of species collected at the bay in front of Lake Camaleão (Junk et al., 1983). Similarly, (Bayley, 1983) found that piscivores contributed to 35% of the total biomass in the system. Thus, predation pressure is a significant factor in the floodplain (Bayley, 1983), partially explaining the intense use of macrophytes as shelter against

predators. Several studies have shown that in response to the presence of piscivorous predators fish shift their microhabitat distribution seeking shelter (Werner et al., 1977; Goodyear, 1973; Seghers, 1974; Stein, 1979). (Tonn et al., 1992) showed that offshore pelagic habitat was underutilized by prey species because of the presence of predators. Roots, leaves and stems provide efficient visual and swimming barriers and mediate the extent by which predators interact with prey (Savino and Stein, 1982), reducing predation rates as habitat structural complexity increases (Crowder and Cooper, 1979; Savino and Stein, 1989).

In addition to providing shelter, macrophytes play an important role in providing food resources. Some species of anostomids and serrassalmins have been reported to feed directly on macrophytes (Paixão, 1980; Goulding, 1980; Santos, 1981; Soares et al., 1986). (Forsberg et al., 1993) noted that although C_4 macrophytes are responsible for approximately half of the primary production in the Amazon floodplain they are not a significant food source for fishes. However, macrophytes do serve as substrate for the development of periphyton (Engle and Melack, 1990), which is a source of high quality organic carbon (Doyle, 1991), and harbor a rich invertebrate community (Junk, 1973; Blanco-Belmonte, 1990; Engle and Melack, 1993). Periphyton and invertebrates associated with macrophytes have been recognized as important food sources for recruiting juveniles of migratory characiforms (Saint-Paul and Bayley, 1979; Goulding, 1980; Goulding and Carvalho, 1982; Araujo-Lima and Hardy, 1987).

Although water physico-chemical parameters varied significantly among the five areas within Marchantaria Island, my results did not support the hypothesis that water physico-chemical parameters by itself directly influenced the distribution of species richness. None of the water chemistry variables measured had a significant effect on species richness and were not retained by the stepwise regression model (Table 2.6). In contrast, species richness was strongly influenced by the proportion of Membeca samples in each of the areas collected within the island (Fig. 2.3), suggesting that habitat structure was the main determining factor in species richness. Nevertheless, because the various macrophytes occurred at a variety of environmental conditions, especially with respect to oxygen concentrations, an interaction between physical habitat characteristics and oxygen concentrations could be involved in determining fish habitat usage within the island's floodplain. Oxygen was found to be a factor limiting species richness in Lake Camaleão, where species richness changed seasonally according to changes in water chemistry (Junk et al., 1983). Nonetheless, because these authors did not clearly specify in which kind of habitat their samples were taken, the results could have been strongly affected by their sampling scheme, masking the influence of habitat on fish diversity.

Fish Assemblages in the floodplain

The relationship of fish assemblage organization in relation to microhabitat conditions in tropical freshwater systems has hardly been addressed. Most studies have analyzed this question at a very broad scale and found no indication of any organizational pattern (Lowe-MacConnell, 1987). In the Amazon floodplain the dynamic aspect of the flood pulse, where environmental conditions change rapidly spatially and temporally during the flood cycle, has led to the postulation that fish assemblages are random in nature (Lowe-MacConnell, 1987; Goulding et al., 1988). My results contrast with this view suggesting that microhabitat characteristics had a strong influence in determining the composition of fish assemblages in the Amazon floodplain. The proportion of variance of fish assemblage's structure explained by the 14 environmental variables retained in the model, 67%, was high compared with most studies that are typified by 40-50 % estimates, despite the pronounced variability in environmental conditions found in the floodplain. The highly significant correlations between water physico-chemical parameters and the species axes suggest that fish assemblages composition were strongly influenced by abiotic factors, which might be the most important forces regulating the spatial and temporal variation in fish assemblages structure during the flooding season in the Amazon floodplain. Fish assemblages in the Amazon floodplain were strongly structured along well-defined environmental gradients, similar to the results obtained for the

Orinoco floodplain (Rodriguez and Lewis, 1997). These results are congruent with the theoretical framework that abiotic factors are more important than biotic interaction in regulating community structure in highly variable and frequently disturbed environments (Menge and Sutherland, 1987).

Environmental gradients of dissolved oxygen, turbidity and depth significantly affected fish and guild distribution, as well as catches within the floodplain (Fig. 2.15; Table 2.10). The effect of macrophyte types on the composition of fish assemblages and catch was also prevalent (Table 2.10). These findings are consistent with the results obtained by Junk et al 1983 for Lake Camaleão in relation to the influence of oxygen on fish distribution. In contrast, (Rodriguez and Lewis Jr, 1994; Rodriguez and Lewis, 1997; Tejerina-Garro et al., 1998) did not find any significant effect of aquatic macrophytes or oxygen concentrations on fish assemblage structure. The only abiotic factors linked to fish assemblage were water transparency and water depth. However, those studies were conducted during the dry season, when oxygen concentrations were high and not a limiting factor (Rodriguez and Lewis, 1997; Tejerina-Garro et al., 1998). The same limnological pattern was observed for Amazon floodplain lakes during the dry season, when oxygen was higher then during the flooding season (Schmidt, 1973). These contrasting results indicate that mechanisms determining structure of fish assemblages in the floodplain have a strong seasonal component related to the flood pulse. As indicated by (Rodriguez and Lewis, 1997), structural cover declines progressively as shorelines recede during the dry season, and fish

become concentrated in a relatively featureless environment. Under these conditions, fish assemblages would be predominantly regulated by biotic interactions such as predation, which is mediated by water transparency in terms of setting underwater visibility (Rodriguez and Lewis, 1997). In contrast, during the flooding season the floodplain environment becomes more complex, offering fish greater structural complexity and diverse microhabitat conditions (Junk et al., 1989). The seasonal dichotomy of biotic and abiotic controls due to the flood pulse has forced plasticity in terms of habitat requirements as well as complex adaptations and behavioral patterns (Junk et al., 1997). During the flooding season abiotic factors can modulate the composition of fish assemblages through differences in physiological tolerance to the physico-chemical environment. Factors such as physiological intolerance to low dissolved oxygen concentrations are directly linked to the absence of some local populations in temperate lakes (Tonn and Magnuson, 1982) as well as in the Amazon (Junk et al., 1983). Morphological, biochemical, and behavioral adaptations allow some species to cope with poor environmental conditions, and allow access to habitats that would otherwise be unavailable (Magnuson et al., 1985).

The distinct distribution pattern among piscivores and detritivores along the first axis of the CCA (Fig. 2.14), corroborate the idea that detritivores have evolved tolerance to hypoxic conditions as an environmental shielding mechanism to reduce predation by using habitats that predators cannot tolerate. Piscivorous predators may also contribute significantly to structuring

fish assemblages in the Amazon floodplain during the flooding season. Diel cycles of habitat use (Saint-Paul and Soares, 1987; Soares, 1993) between open water and macrophyte stands suggests that prey species avoid predation during the day by hiding inside macrophyte stands, despite the hypoxic conditions inside these stands. Most pelagic piscivorous predators are intolerant to hypoxic conditions (Junk et al., 1997) and remain restricted to areas where oxygen concentrations are higher, whereas many prey species tolerate very low oxygen concentrations through morphological, behavioral or biochemical adaptations (Braum and Junk, 1982; Kramer and McClure, 1982; Saint-Paul, 1984; Saint-Paul and Soares, 1988). In Lake Camaleão several detritivores use both protected areas covered by macrophytes and open water habitat in the absence of predators (Soares, 1993). This indicates that these species explore a wider habitat spectrum when predators are not present. Similar patterns were also found in temperate lakes (Stein, 1979; Tonn et al., 1992).

Combining the results of the CCA and indicator species analysis reveals that fish assemblages in the Amazon floodplain are relatively predictable at small scales. Species associations seem to be largely influenced by the combination of habitat structural characteristics and the underlying water chemistry variables. Several species showed strong preference for particular macrophytes (Table 2.13). *Auchenipterus nuchalis, Hyphessobrycon calisticus, Parauchenipterus galeatus* and *Synbranchus marmoratus*, occurred predominantly in *Eichhornia crassipes* stands and were

mostly absent from other habitats. The detritivores *Prochilodus nigricans,*

Semaprochilodus insignis, Semaprochilodus taeniurus, Liposarcus pardalis

and *Hoplosternum litorale,* showed a strong tendency to be associated with

murim and canarana stands, especially in areas with oxygen deficiency (Fig.

2.15 Table 2.13, Table 2.14). These results suggest some degree of habitat

selectivity by groups of species for particular macrophyte coverage under

particular environmental conditions. In contrast to that, none of the pelagic

predators showed any affinity for a particular macrophyte showing a more

ubiquitous distribution in relation to habitat structural characteristics (Table

2.13).

As shown herein and by several previous studies, aquatic macrophytes

are an integral component of the life cycle of many species of fishes that

occur in the Amazon floodplain. It is most likely that alteration of the

distribution and abundance of aquatic macrophytes could have a significant

impact on the ichthyofauna of the floodplain. The extensive removal of

macrophytes would reduce habitat complexity, increasing unstructured open

water areas that were shown to be poor habitat for floodplain fishes. The

recent intensification of human use of the floodplain can potentially alter the

dynamics of the floodplain environment. Land use for small commercial

vegetable farming at Marchantaria Island has triggered the removal of flooded

forest and significant alteration of macrophytes stands by burning during the

dry season (pers. Observation). Cattle ranching along the Amazon floodplain

has triggered the harvest of aquatic macrophytes to serve as food for cattle

(McGrath et al., 1993). In addition, the introduction of water buffalo and the herd's fast growth (600 % increase between 1974 and 1984) has reduced the aquatic vegetation by the direct foraging (McGrath et al., 1993). There are no published studies that have established causal relationship between cattle ranching practices in the floodplain and its impact on fish production, nevertheless there are indications of such impact in the lower Amazon (Câmara and McGrath, 1995). The two most impacted species of aquatic macrophytes are *Echinochla polystachya* (canarana) and *Paspalum repens* (Membeca), both very important nursery habitats for many species of migratory Characiformes (Goulding, 1980; Bayley, 1983; Junk, 1984).

In order to maintain the stability, functioning and productivity of the floodplain system it is imperative that serious attention should be directed towards analyzing the impacts of human land use in the floodplain. The implementation of development projects that may alter this ecosystem should be scrutinized rigorously to prevent serious losses in fish production and biodiversity in the floodplain.

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Chapter 3

Morphology, Shape Analysis and Microincrement Analysis of Serraslmin Fishes Otolith's

Abstract

The morphology, ontogenetic development, shape variability and deposition of otolith microincrements are described for Amazon River floodplain dwelling serralmin fishes. Serrasalmin otoliths have the general morphology of other ostariophysans; nevertheless their shape was found to be species- specific. Elliptical Fourier analysis showed that *Mylossoma aureum* lapilli were highly variable in shape when compared to closely related species. Results from PCA and discriminant function analysis indicated that two distinct forms of lapillus can be recognized for M. aureum, and that intra-species variation was higher than inter-species variation. The use of otolith microincrement analysis was tested for these fishes, and microincrement deposition validation showed that *Piaractus brachipomus* deposits otolith increments on a daily basis.

Introduction

In the thirty years since (Pannella, 1971) described daily microincrements on otoliths of fishes, most research has focused on temperate and tropical marine fishes. Otolith morphology, microincrements and chemical composition have been used for studies on ageing, growth, population demography, ontogenetic development, recruitment processes, stock identification, and reproductive schedules. The chronology of increment deposition, the relationship between somatic growth and otolith growth, and the physiological and biochemical processes of increment formation have been studied extensively (Tanaka et al., 1981; Rosa and Ré, 1985; Gauldie and Nelson, 1990; Mugiya and Tanaka, 1992).

Otolith morphology differs among taxonomic groups, but is sufficiently conservative to be used for species identification in paleontological studies, marine mammal dietary studies, and in conventional taxonomic descriptions (Nolf, 1985; Sideleva and Zubina, 1990; Schmidt, 1969; Gaemers, 1984; Gauldie, 1988). More recently, otolith morphology has been used to describe intraspecific variations among fish populations. Jarvis et al., (1978) proposed using Fourier transformations to quantify otolith shapes to differentiate fish stocks. Fourier transformations describe the outline of a shape using a series of sinusoids (harmonics), which are characterized by amplitude and a phase angle. Because of their orthogonality, harmonic amplitudes can be uses with several types of multivariate analysis (Rohlf and Archie, 1984; Ferson et al.,

1985; Castonguay et al., 1991). Stock discrimination studies based on Fourier descriptors show that shape differences in herring otoliths are related to races and age groups (Bird et al., 1986), whereas shape differences in cod otoliths are related to age, sex, year class and race (Campana and Casselman, 1993). A central issue in many studies is increment validation for aging (Geffen, 1992), especially for species or taxa previously un-studied. Validation of daily increment deposition has usually been performed using larvae or juveniles of known age, or by marking otoliths of fishes with unknown ages (Taubert and Coble, 1977; Jones and Brothers, 1987; Tzeng and Yu, 1988; Tzeng and Yu, 1989; Geffen, 1992). Fluorescent chemicals, such as oxytetracycline, calcein fluorescent green and Alizarin complexone, can be metabolically incorporated into calcifying structures (Schmitt, 1984; Tsukamoto, 1988; Thomas et al., 1995). Treatments usually employ immersion (Secor et al., 1991b), direct injection (Thomas et al., 1995), or oral administration (Marking et al., 1988; Thomas et al., 1995).

Ostariophysan fishes (minnows, characins, catfishes and suckers) have a unique inner ear morphology, (Frost, 1925; Adams, 1940) based in part in the position, shape and relative size of otoliths (Adams, 1940; Rosen and Greenwood, 1970). Although ostariophysans are the predominant group of freshwater fishes throughout the world and commercially important, there are few studies of otolith development and microincrement validation (Mugiya and

Tanaka, 1992; Thompson and Beckman, 1995; Hoff et al., 1997), and none

for South American Characiformes.

The purpose of this study is to describe otolith morphology and

development and to validate increment deposition rate in South American

serrasalmins. Ontogenetic changes in all three otoliths are described for *M.*

aureum and the relationship between somatic growth and lapillus growth is

described. The morphology of the right lapillus is described using elliptic

Fourier analysis for five taxa (*Piaractus brachipomum*, *Colossoma*

macropomum, *Mylossoma duriventri*, and two forms of *M. aureum*). Daily rate

of otolith microincrement deposition is validated for *P. brachipomum*.

Methods

Otolith development and microstructure

The three pairs of otoliths (asteriscus, lapillus and sagitta) from wild-

caught, *M. aureum* at 14mm, 22mm and 49 mm SL were examined to

describe their ontogenetic development, determine shape changes and

suitability for ageing. After extraction, otoliths were soaked in distilled water,

cleaned of adhering tissue, dried at room temperature and mounted on glass

slides using Crystalbond 509 thermoplastic media. (Secor et al., 1991a).

Terminology for otolith morphology generally followed (Kalish et al., 1995) and

(Weitzman, 1962). Lapilli from 734 wild-caught, ethanol-preserved M. aureum

(12-50 mm SL) were used to extract otolith morphometric data. Lapillus area,

maximum length and outer perimeter outlines were obtained from whole

mounts with the ventral surface up using Optimas 5.0 image analysis system,

attached to a Leitz Laborlux compound microscope with 2.5 and 4 X

objectives. Anterior and posterior lobe lengths were obtained from sagittal

plane sections.

Shape analysis

Right lapilli of 230 *Mylossoma aureum*, 33 *M. duriventri*, 11 *Colossoma*

macropomum, and 22 *Piaractus brachipomus* between 30 and 90 mm SL

were analyzed. Whole Lapilli outlines were digitized with Optimas 5.0 using

an edge detection algorithm with a variable gray-scale threshold under

polarized light to enhance edge contrast and increase the resolution of outline

tracing. Five hundred twelve pairs of evenly spaced Cartesian coordinates

were used to describe the outlines. Lapillus shape variation was analyzed by

orthogonal decomposition into a sum of harmonically related ellipses, in a two-

dimensional elliptic Fourier analysis (EFA) (Kuhl and Giardina, 1982; Ferson

et al., 1985) using EFAWIN V.1.0 (Isaev, 1995). The function has a Fourier

expansion into terms of sine and cosine curves of integer frequencies with

appropriate amplitudes (Ferson et al., 1985). Because EFA is a two

dimensional decomposition, it generates four coefficients per harmonic,

instead of two obtained by fast Fourier transforms. Coefficients a and b are cosine and sine functions projected onto the X-axis, whereas and c and d are cosine and sine projections onto the Y-axis (Kuhl and Giardina, 1982). Harmonic coefficients were normalized to be invariant to size, location, rotation, and starting point of the trace, to extract pure shape information. This transformation caused the degeneration of the first three coefficients of the first harmonic, which become constant (a_1=1, b_1=0, c_1=0) thus making them trivial to the analysis (Rohlf and Archie, 1984; Ferson et al., 1985). These coefficients were eliminated from the subsequent data set. A total of 37 non-trivial harmonic coefficients were retained. Normalized coefficients were arranged as a column vector (d_1, a_2,b_2,c_2,d_2, a_3,b_3,..., b_N,c_N,d_N,), and used as a multivariate point representing the outlines in a (4N-3) dimensional shape space of potential variation (Ferson et al., 1985). Sequential removal of uninformative coefficients from principal component analysis (PCA) eliminated the d coefficient of the first harmonic and all coefficients of harmonics 8-10, resulting in 24 informative coefficients (2nd to 7th harmonic). Condensed harmonic coefficients were calculated from this data set, creating two coefficients per harmonic, $\Delta x_n = SQRT (a_n^2 + b_n^2)$ and $\Delta y_n = SQRT (c_n^2 + d_n^2)$.

Two distinct otolith shape groups within *M. aureum* were described using PCA of the 24 informative coefficients and a one-way analysis of variance (ANOVA) of the condensed harmonic coefficients. A discriminant function analysis (DFA) of the 24 informative coefficients was then used to

describe shape differences between the four species and two forms of *M. aureum*. All statistical analyses were performed using SYSTAT 5.0 (Wilkinson, 1990).

Validation of increment deposition rate

Experiments

Microincrement validation experiments were conducted using twenty-seven juveniles of *P. brachipomus* (48 - 60 mm SL) of unknown age, obtained from a commercial fish dealer. Fish were acclimated in four 10-gallon glass aquaria for one week at a constant 28 °C and a 12-hour light cycle. Each specimen was anaesthetized, measured to the nearest 0.1 mm, weighted to the nearest 0.1g, and marked with a numbered tag attached at the insertion of the dorsal fin.

In experiment no. 1, specimens were immersed Aug 7, 1991 for 24 hr in 500 mg/l Oxytetracycline Hydrate (OTC) in calcium free water, buffered with sodium bicarbonate to pH 7.5 (Tzeng and Yu, 1989). After immersion, fish were returned to clean tap water tanks. Four fish were sacrificed after five days, and four after ten days. On Aug 22 the remaining nineteen fish were divided into two groups, with 10 receiving a second immersion dose of OTC as above, and nine receiving an oral dose of OTC at 150 mg/kg of fish weight. Two fish of each group were sacrificed fifteen days later. On Sep 13 the 15 remaining fish received an intraperitonial injection of OTC equivalent to 150

mg/kg of fish weight. The volume injected ranged from 0.03 to 0.15 ml. Four

fish were harvested ten days later, and the remaining eleven fish were

sacrificed 29 days later.

In experiment no. 2, nine fish (45 - 76 mm SL) received intraperitonial

injections on four days (Dec 3 1991, Dec13 1991, Jan 15 1992 and Mar 20

1992). All fish were harvested Mar 23. During both experiments fish were fed

with commercial fish pellets to satiation once a day.

Otolith preparation and analysis

Immediately after harvesting fish, all three pairs of otoliths were

removed as above and stored in glass vials in the dark. OTC marked otoliths

were placed in embedding media in a dorso-ventral orientation and cured for

12 hs at 65 °C to allow media polymerization. Embedding blocks were

mounted on to glass slides with Crystalbond 509. Three preparations,

modified from (Secor et al., 1991a), were used to determine the most

appropriate preparation for microincrement analysis: longitudinal sections,

transverse sections, or dorso-ventrally ground sagittal plane sections. All

preparations included initial grinding with 600 grit paper, finish grinding with

2,000 grit, and polish with 0.5 μ wet alumina powder. Increment widths (3 to

7.6 μm) on lapillus were well above light microscopy resolution limits

(Campana and Neilson, 1985), therefore, light microscopy was appropriate for

microincrement analysis in these fish. Otoliths were examined on a Zeiss

universal epi-fluorescence microscope with a 75-watt xenon lamp, 15x wide-angle eyepiece lenses, and 16x or 40x neofluor objective lenses. Two sets of epi-fluorescence filters were used to produce the OTC fluorescent bands. DAPI set 477702 (G 365 excitation filter, FT 395 beam splitter and LP 420 barrier filter) with near UV excitation and blue emission; and FITC set 487709 (BP 450-490 excitation filter, FT 510 beam splitter and LP 520 barrier filter) with blue excitation and apple green emission. A combination of transmitted light and incident blue or UV light was used to locate areas on the preparation where microincrements and fluorescent bands could be distinguished. Photographic slides were taken at 600x from each preparation in different light intensity combinations to allow for a *posteriori* tracing of microincrements and fluorescent marks. OTC mark quality and retention was assessed using a qualitative method by recording presence or absence and by ranking the intensity of mark. Increment counts were made between fluorescent marks and between the last fluorescent mark and the otolith edge. Otoliths were read thee times on separate dates by the same reader.

Distances between OTC marks were obtained using a calibrated eyepiece micrometer, and measured along the anterior- posterior longitudinal axis for longitudinal and sagittal sections. Total length, anterior length (maximum distance between primordium and anterior edge) and posterior length (maximum distance between primordium and posterior edge) were measured using Optimas 5.0 image analysis system. Simple linear regression

analysis was used to test the relationship between number of increments and number of days elapsed since marking. A slope comparison test was used to verify whether the regression slope was different than 1.0 (Neter et al., 1989). Linear regression analysis was also used to analyze the relationship between somatic growth and otolith growth, and the overall relationship between fish size and otolith size.

Results

<u>Otolith development and microstructure</u>

Otoliths of *M. aureum* were morphologically similar to other ostariophysi (Frost, 1925; Adams, 1940). The asteriscus, the largest of the three pairs, was encased in a bony capsule formed by a ventro-lateral projection of the exoccipital and basioccipital bones. In small specimens (12-14 mm SL) the asteriscus was sub-circular and "drop-like" with a acentric primordium located close to the ventral edge and smooth anterior and posterior borders (Fig. 3.1a). Ontogenetically, it became star-shaped with a pronounced rostral process that projected anteriorly forming a deep groove (Fig. 3.1b,c; Fig. 3.2a,b). The lateral face was concave and granular with a series of radial furrows extending from the center toward the edges. In juveniles (>45 mm SL) the crests of the radial furrows formed serrations on the posterior edge (Fig. 3.2a). The medial face was convex with a deep sulcus opening at the

base of the rostral groove and encircling about 2/3 of its surface (Fig. 3.2b).

Asteriscus microincrements could be recognized in longitudinal cross sections

and sagittal plane preparations, but counts were inconsistent. Longitudinal

cross sections showed the primordium located off center, closer to dorsal

surface. Increment deposition appeared complex, with deposition in a

downward angle in relation to the position of the primordium Fig. 3.3a. The

sagitta lies in the saccular recess, a bony cavity formed by the prootic,

basioccipital and exoccipital. The anterior end was inserted into a bone

pocket of the prootic, while the posterior end reached the chamber that

accommodates the asteriscus. Ostariophysan sagittae are noticeably

different from other teleosts, but most closely reflect the name, sagitta or

arrow-like being extremely elongate with a flat profile, which becomes

accentuated during ontogeny (Fig. 3.1d,e,f). Two thin processes expanded

laterally from the mid-region to form a flat, elongated "paddle-like" rostrum

that projected anteriorly. The posterior cylindrical, "blade-like", and ended in a

sharp edge. A longitudinal ridge extended on the lateral face, perpendicular

to the lateral processes, forming a thin medial shelf, similar to the one

described for *Brycon meeki* (Weitzman, 1962). The medial face of the sagitta

is smooth without any distinctive feature (Fig. 3.2e). Because of its flat and

elongated shape, the sagitta did not allow for good, high-resolution sagittal

plane preparations.

anterior
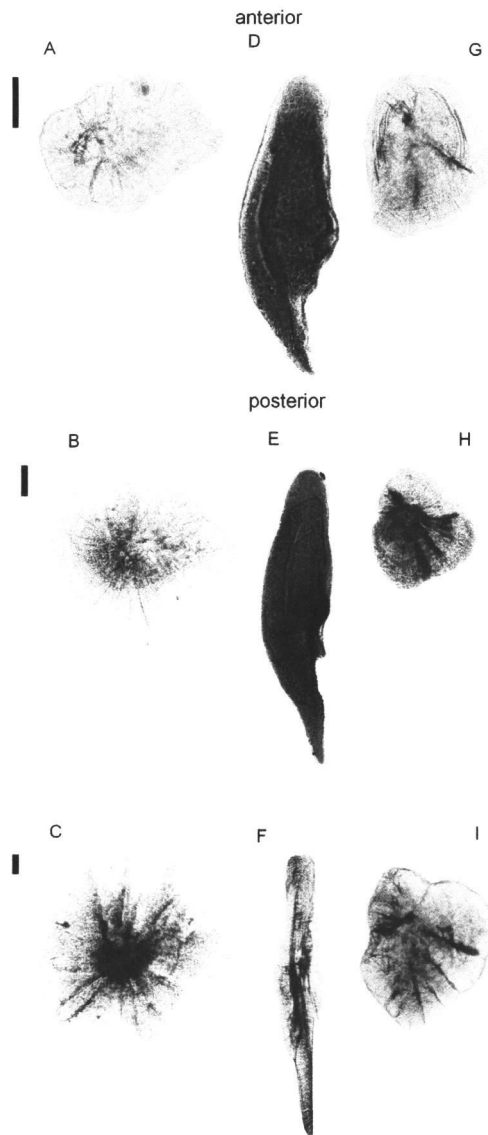
posterior

Figure 3.1. Ontogenetic developmental series of the three pairs of otoliths (asteriscus, sagitta and lapillus) of *Mylossoma aureum*. Otoliths are oriented in an antero-posterior direction. Developmental series from the top to the bottom, 14 mm SL, 22mm SL and 49 mm SL. Asteriscus developmental series (a, b and c), sagitta developmental series (d,e and f) and lapillus developmental series (g, h and i). Scale bars represent 150 microns.
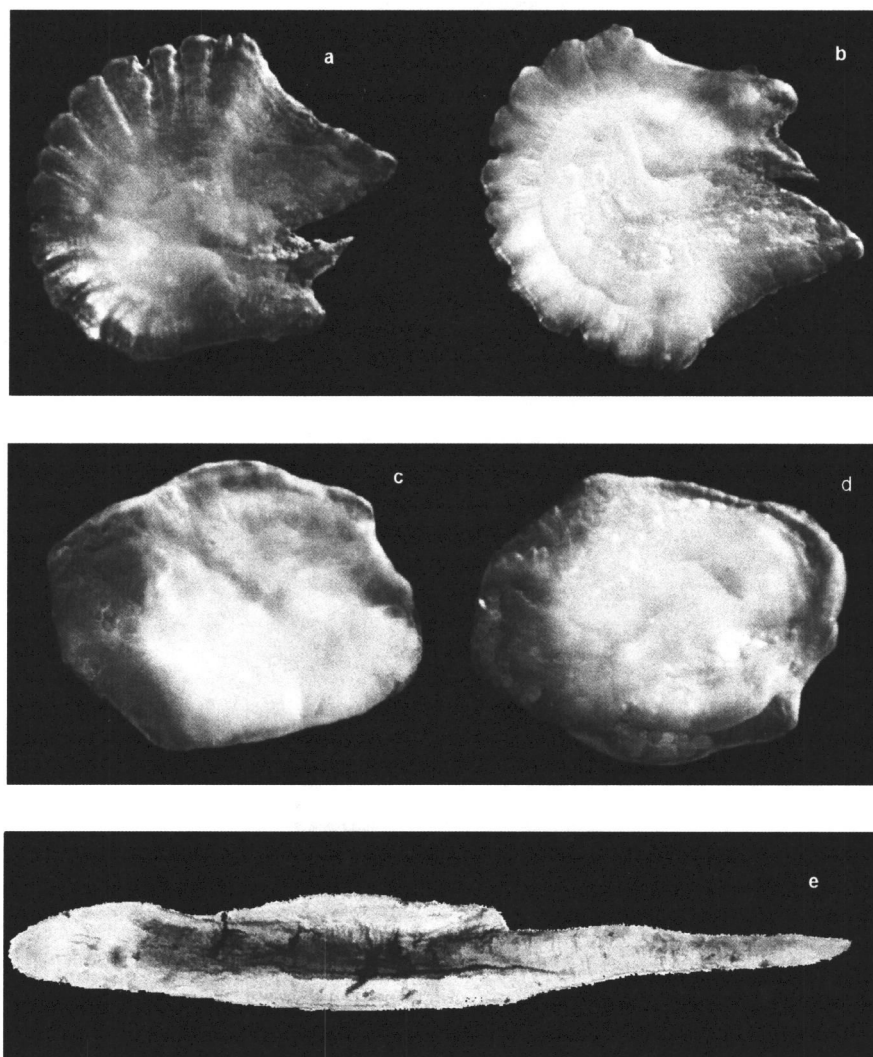
Figure 3.2. Right otoliths of *Mylossoma aureum*; (a) asteriscus lateral face, (b) asteriscus medial face, (c) lapillus lateral face, (d) lapillus medial face and (e) sagitta dorso-medial face.

Cross sections were possible, but were unsuitable for microincrement analysis because of the complex nature of microincrement deposition.

The lapillus lays flat on its side in the utricular sac on the floor of the prootic bone, at a 90-degree angle to the other otolith pairs. The lapillus in

small specimens (14 mm SL or less) was oval, with the primordium located slightly off center closer to the anterior border (Fig. 3.1g).
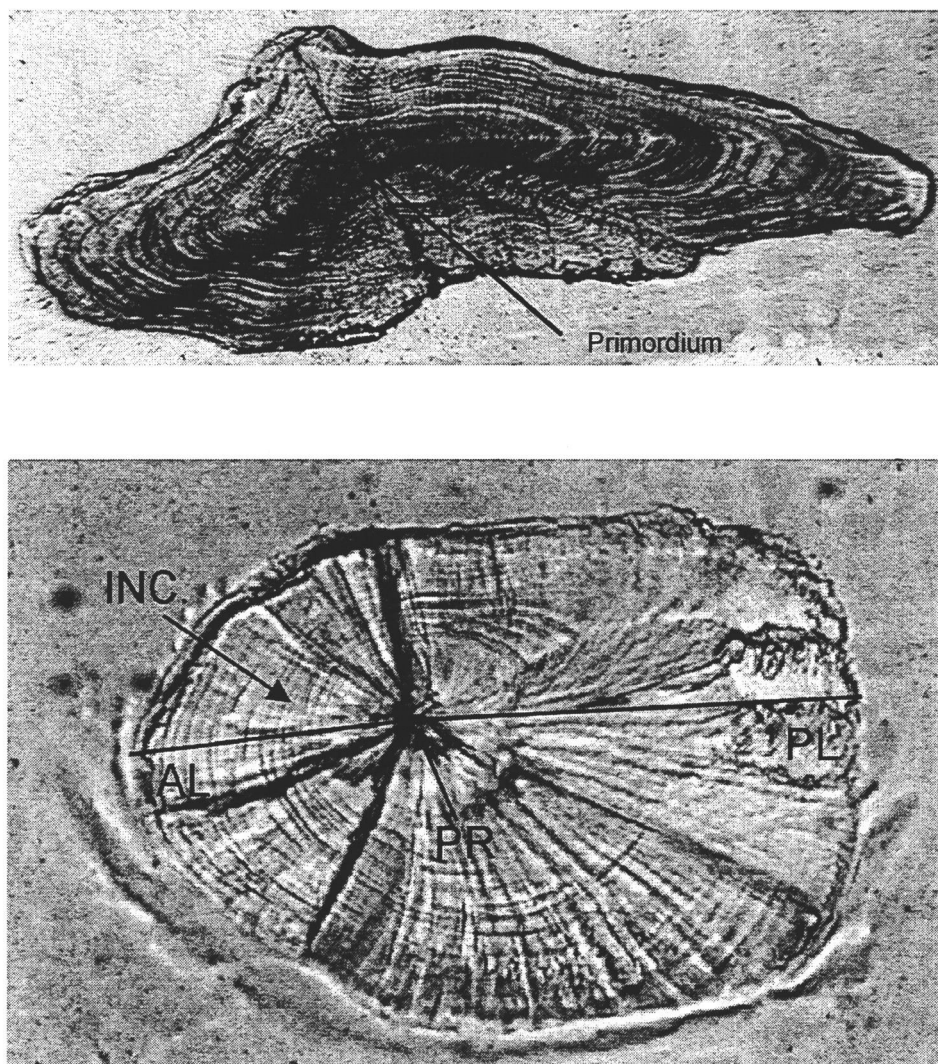
Figure 3.3. Transversal cross section of the asteriscus, showing the complex deposition of microincrements, (a). Sagittal section of the lapillus of *Mylossoma aureum* (b), (AL) anterior length, (PL) posterior length, (PR) primordium and (INC) microincrements.

Between 15-25 mm SL a medial process developed, the lapillus expanded laterally, and the anterior lobe became more pronounced (Fig. 3.1h). In larger juveniles (>50 mm SL) the medial process became larger relative to the anterior lobe and developed a posterior scalloped margin. The ventral face was convex and had a distinct sulcus that surrounded the borders of the anterior lobe, whereas the dorsal face was concave and granulated without any distinct features (Fig. 3.2c,d). Longitudinal cross sections and sagittal plane sections consistently yielded unambiguous, high-contrast, recognizable microincrements on the anterior lobe across all fish sizes. Increment widths in fish from 12 - 45 mm SL ranged from 3.5 - 10µ (Fig. 3.3b). Microincrement counts on the posterior lobe were also consistent but less recognizable and relatively wider.

Lapillus length and area were strongly related to size in *M. aureum* (Table 3.1). The relationship between lapillus length and SL was: Lapillus length= -0.06+0.028*SL (R^2 = 0.979, n=734) (Fig. 3.4a). Both anterior and posterior lobes were proportional to size, although the average length of the posterior lobe was 71% greater than the anterior lobe in fish 12-50 mm SL. The relationships were: anterior lobe length= 0.01*SL (R^2 = 0.931, n=734) (Table 3.1, Fig. 3.4b); and, posterior lobe length= -0.049 +0.019*SL (R^2 = 0.958, n=734) (Table 3.1, Fig. 3.4c). Square root of lapillus area was also strongly correlated to fish size: lapillus area= $(-0.022 + 0.021*SL)^2$ (R^2 = 0.981, n=734) (Table 3.1, Fig. 3.4d).

Table 3.1. Linear regressions for the relationship between SL and lapillus size in *M. aureum*: otolith total length (OtL), length of the anterior lobe (AL), length of the posterior lobe (PL) and lapillus area (OtA).

OtL

Parameter	Estimate	std. error	t-value	Sig.level	
Intercept	-0.063	0.005	-12.64	0.0000	
Slope	0.029	0.000	187.14	0.0000	
Analysis of Variance					
Source	SS	Df	MS	F-Ratio	Sig.level
Model	87.594	1	87.59	35020.04	0.0000
Residual	1.833	733	0.003		
Total (Corr.)	89.428	734			
R-squared	0.979				
Std. Error of Est.	0.050				

AL

Parameter	Estimate	std. error	t-value	Sig.level	
Intercept	0.000	0.0031	0.0003	0.99977	
Slope	0.010	0.0001	99.7418	0.0000	
Analysis of Variance					
Source	SS	Df	MS	F-Ratio	Sig.level
Model	9.657	1	9.66	9948.42	0.0000
Residual	0.711	733	0.001		
Total (Corr.)	10.368	734			
R-squared	0.931				
Std. Error of Est.	0.031				

PL

Parameter	Estimate	std. error	t-value	Sig.level	
Intercept	-0.049	0.0046	-10.55	0.0000	
Slope	0.019	0.0001	130.85	0.0000	
Analysis of Variance					
Source	SS	Df	MS	F-Ratio	Sig.level
Model	36.897	1	36.897	17121.83	0.0000
Residual	1.580	733	0.002		
Total (Corr.)	38.477	734			
R-squared	0.958				
Std. Error of Est.	0.046				

OtA (*sqrt of area*)

Parameter	Estimate	std. error	t-value	Sig.level	
Intercept	-0.033	0.0036	-9.2335	0.0000	
Slope	0.021	0.0001	195.4390	0.0000	
Analysis of Variance					
Source	SS	Df	MS	F-Ratio	Sig.level
Model	48.391	1	48.391	38196.27	0.0000
Residual	0.929	733	0.00127		
Total (Corr.)	49.320	734			
R-squared	0.981				
Std. Error of Est.	0.036				
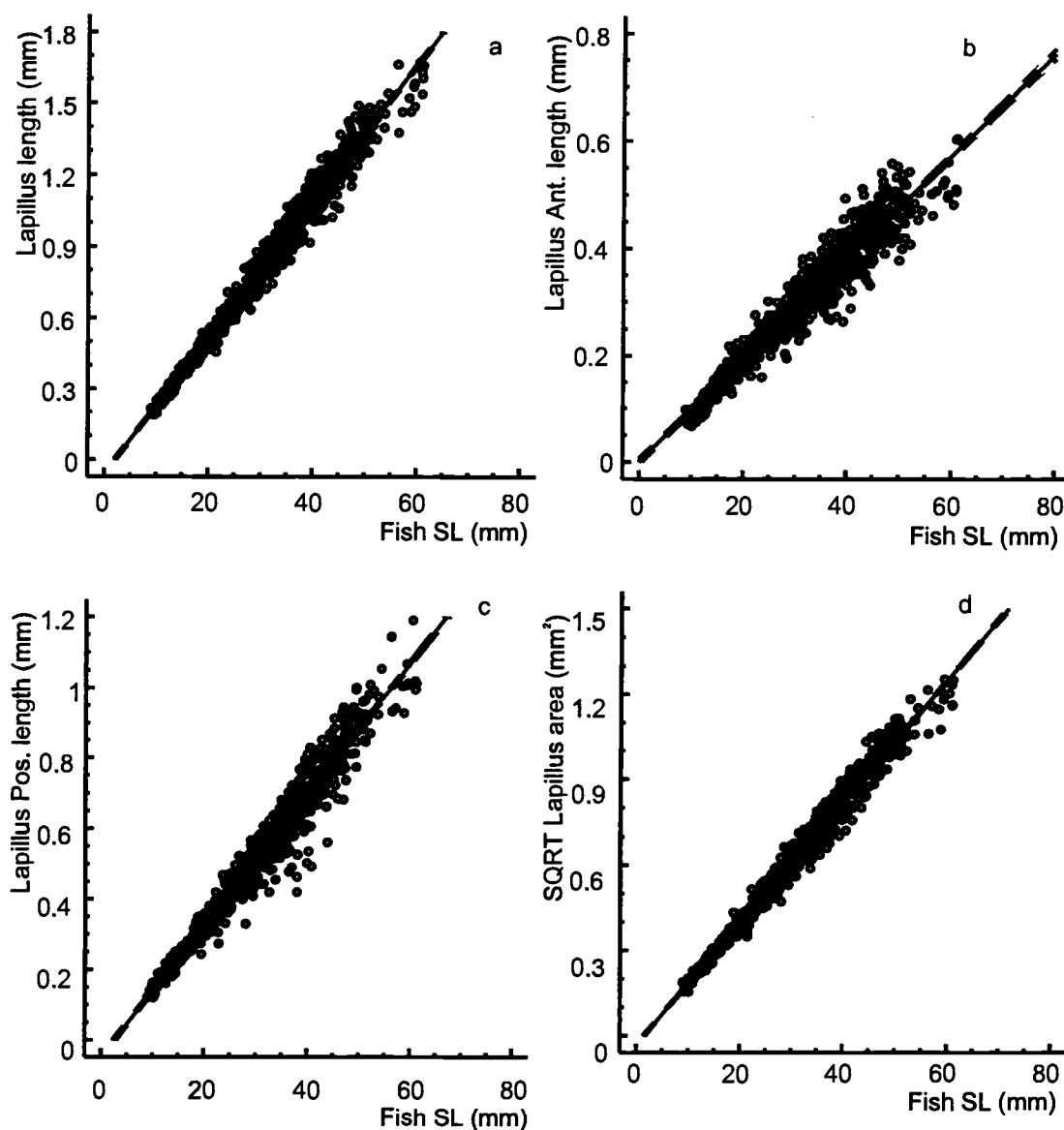
Figure 3.4. Relationships between fish length and lapillus morphometric measurements in *Mylossoma aureum*. Relationship between SL and lapillus total length (a); between SL and anterior lobe length (b), between SL and Lapillus posterior region length(c) and between SL and lapillus area (d).

Lapilli were chosen for all subsequent analyses, and because sagittal sections of the anterior lobe were consistent and easily obtained, that section and region and were chosen for subsequent ageing analyses.

Shape analysis

Lapilli had species-specific shapes (Fig. 3.5). The greatest intraspecific shape variation was seen in *M. aureum*, which had two distinct shape groups, types (a) and (b). Type (a) had a rounded shape without a pronounced notch between the anterior lobe and lateral process (Fig. 3.5d). Type (b) had a more oval, elongate shape and a pronounced notch between the anterior lobe and lateral process (Fig. 3.5e). The angle between the anterior lobe and the lateral process was more than 90 degrees in Type (a) (Fig. 3.5d) and equal to or less than 90 degrees in Type (b) (Fig. 3.5e). The 24 informative harmonic coefficients in the elliptical Fourier analysis accounted for more than 95% of the original shape reconstruction for all five forms (Fig. 3.6). Lower order harmonics (2 to 4) were the most variable (Fig 3.7) and *M. aureum* (both types pooled) had the highest variance for harmonics 2, 3 and 4 (Fig. 3.7a). Higher order harmonics (5-10) had low variance for all species except for a slightly higher value for *C. macropomum* for harmonic 6 (Fig. 3.7c). Results of the PCA of the 24 informative harmonic coefficients for *M. aureum* are shown in Table 3.2. Harmonic coefficient *a* was important along the first PC axis with
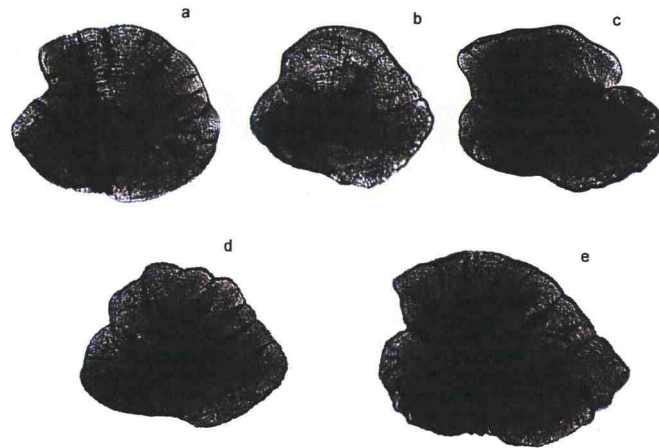
Figure 3.5. Right lapilli of: (a) *Colossoma macropomum*, (b) *Mylossoma duriventri*, (c) *Piaractus brachipomus*, (d) *Mylossoma aureum* type (a) and (e) *M.aureum* type (b).
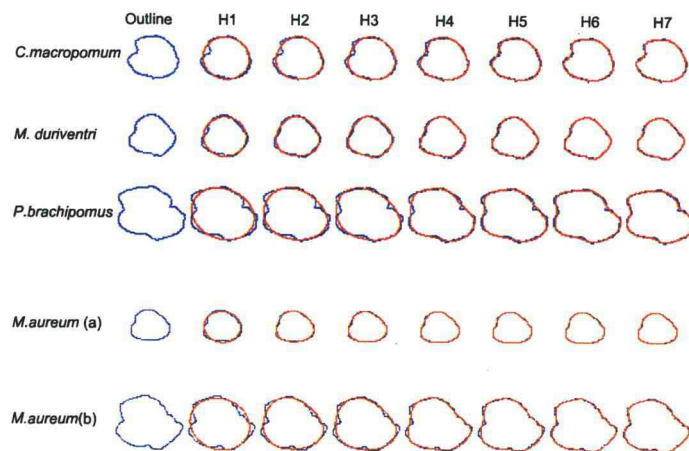
Figure 3.6. Elliptic Fourier outline reconstruction of the lapillus using the cumulative fitting of harmonics. Blue lines represent the original outlines described by 512 pairs of coordinates, red lines represent the fitting by the addition of subsequent harmonics, from second to seventh.

coefficients 3a, 5a and 7a having negative scores and coefficients 2a, 4a and

6a having positive scores (Table 3.2; Fig. 3.8a). Type (a) otoliths had

negative scores and type (b) had positive scores on PC axis 1 (Fig. 3.8b).

Condensed coefficients, Δ_x and Δ_y, were significantly different between the two

types (Table 3.3). Harmonic 3 had significant differences for both coefficients

, Δ_{x3}, (F=62907, p<0.001) and Δ_{y3} (F=7489, p=0.0068). Harmonics 6 and 7

had significant differences for the Δ_x coefficient, whereas harmonic 4 had

significant differences for the Δ_y coefficient (Fig. 3.9).
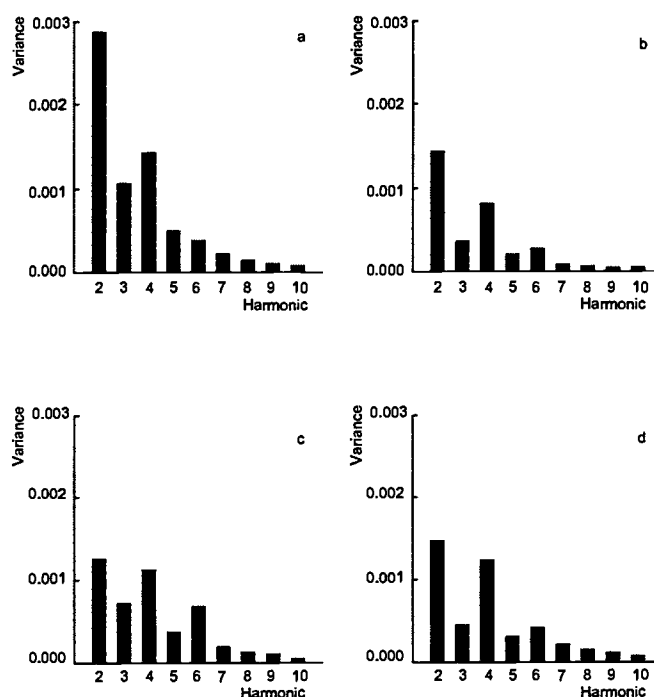
Figure 3.7. Plot of harmonic variances the elliptic Fourier analysis. Variances per harmonic are given as the sum of the variances of the 4 coefficients for each harmonic. The four species are: (a) *Mylossoma aureum*, (b) *Mylossoma duriventri*, (c) *Colossoma macropomum* and (d) *Piaractus brachipomus*.

Table 3.2. Principal components analysis *of M. aureum* otoliths shape descriptors using two-dimensional elliptic Fourier analysis. Percentage of total variance explained by the first five canonical axis and harmonic coefficients loadings on each canonical axis.

Canonical Axis	1	2	3	4	5
Eigenvalues	7.69	3.66	2.64	1.95	1.37
% variance explained	32.37	15.16	11.90	7.80	5.35
Cumulative percentage	32.37	47.53	59.44	67.24	72.60
			loadings		
Coefficient	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
BH4	0,865	-0,266	-0,031	0,207	0,133
AH5	-0,85	0,023	0,337	0,04	0,141
AH7	-0,807	0,005	-0,036	0,16	0,057
BH6	0,768	-0,279	0,327	0,141	0,199
CH6	0,758	0,141	0,07	0,018	0,154
AH4	0,707	0,581	0,118	-0,151	0,042
CH2	-0,67	0,176	0,046	-0,038	-0,105
DH3	-0,646	0,097	0,443	-0,019	0,091
AH2	0,64	0,377	0,003	0,365	0,034
DH4	-0,631	-0,105	-0,353	-0,48	0,16
BH2	0,587	-0,353	-0,483	0,261	0,087
CH5	-0,584	0,1	0,097	0,501	0,17
AH3	-0,582	-0,142	0,395	0,104	-0,092
CH7	0,574	0,326	0,013	0,165	-0,348
AH6	0,569	0,374	-0,177	-0,5	0,256
BH5	-0,116	0,858	-0,163	0,297	-0,226
CH3	0,131	-0,679	-0,387	-0,148	-0,033
BH7	-0,098	0,675	-0,484	-0,25	-0,18
DH6	0,233	-0,559	0,111	0,525	-0,022
BH3	-0,341	0,509	-0,355	0,597	-0,002
CH4	-0,319	-0,297	-0,652	0,13	-0,312
DH2	0,413	0,36	0,613	-0,08	-0,107
DH5	-0,051	0,221	-0,545	0,161	0,474
DH7	0,263	-0,261	0,006	-0,089	-0,756

Table 3.3. Analysis of variance of the condensed harmonic coefficients for the two types of otolith shapes within *M. aureum.* Δ_{xn} and Δ_{yn} are the projections onto the x and y axes for each harmonic, from second to seventh.

Coefficient	Source of variation	S	d.f.	MS	F-ratio	Sig. level
Δ_{x2}	Between groups	.0000	1	8.40E-5	.301	.5898
	Within groups	.0564	202	2.79E-4		
	Total (corrected)	.0565	203			
Δ_{y2}	Between groups	.0000	1	7.85E-5	.246	.6260
	Between groups	.0059	1	.005	62907	.0000
	Within groups	.0192	202	.00009		
	Total (corrected)	.0252	203			
Δ_{y3}	Between groups	.0011	1	.001	7489	.0068
	Within groups	.0305	202	.0001		
	Total (corrected)	.0316	203			
Δ_{x4}	Between groups	.0000	1	5.3E-5	.505	.4859
	Within groups	.0213	202	1.05E-4		
	Total (corrected)	.0213	203			
Δ_{y4}	Between groups	.0023	1	.002	20777	.0000
	Within groups	.0226	202	.0001		
	Total (corrected)	.0249	203			
Δ_{x5}	Between groups	.0000	1	9.74E-5	1743	.1883
	Within groups	.0113	202	5.59E-5		
	Total (corrected)	.0113	203			
Δ_{y5}	Between groups	.0000	1	4.44E-5	1427	.2337
	Within groups	.0062	202	3.11E-5		
	Total (corrected)	.0063	203			
Δ_{x6}	Between groups	.0018	1	.0018	42284	.0000
	Within groups	.0088	202	.00004		
	Total (corrected)	.0107	203			
Δ_{y6}	Between groups	.0000	1	4.79E-5	1819	.1789
	Within groups	.0053	202	2.63E-5		
	Total (corrected)	.0053	203			
Δ_{x7}	Between groups	.0001	1	1.01E-4	4903	.0279
	Within groups	.0041	202	2.06E-5		
	Total (corrected)	.0042	203			
Δ_{y7}	Between groups	50E-	1	5.37E-7	.043	.8384
	Within groups	.0025	202	1.25E-5		
	Total (corrected)	.0025	203			
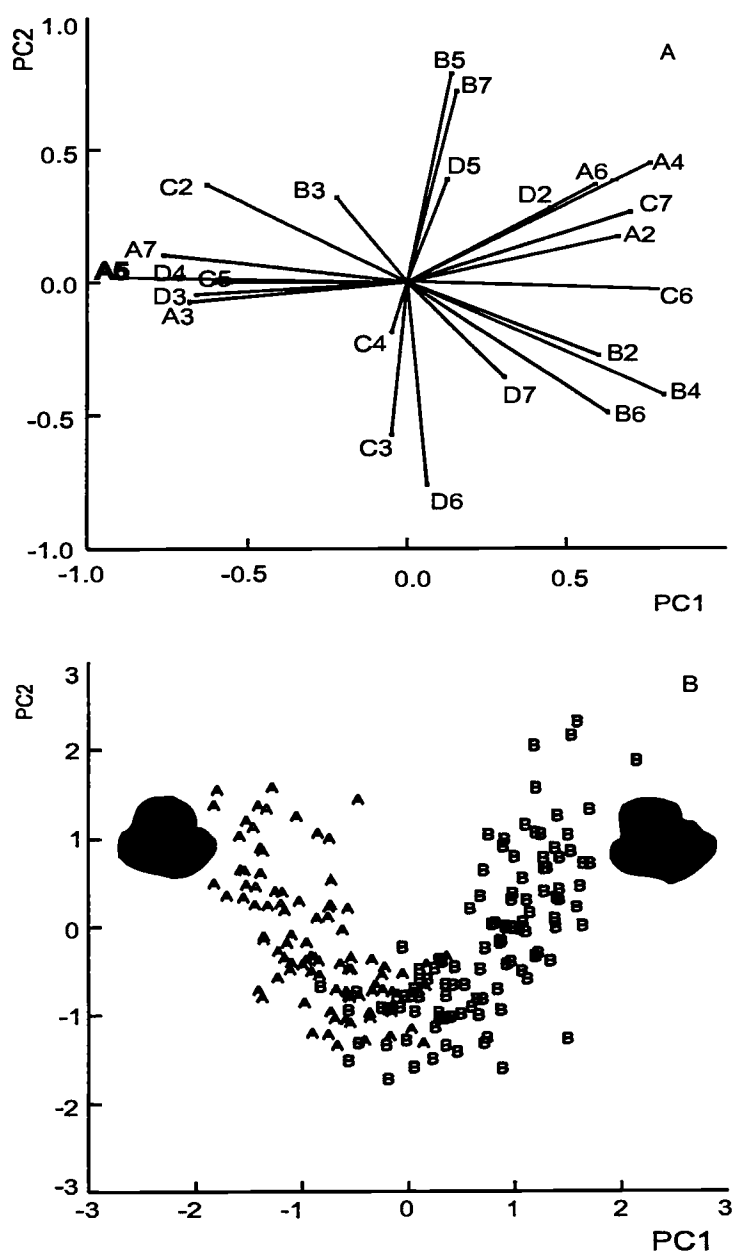
Figure 3.8. PCA plots of *Mylossoma aureum* lapillus shape analysis. (A) harmonic coefficient loadings on to the first two principal components; (B) scatterplot of pca scores for the first two components. A's and B's represent the two shape types.
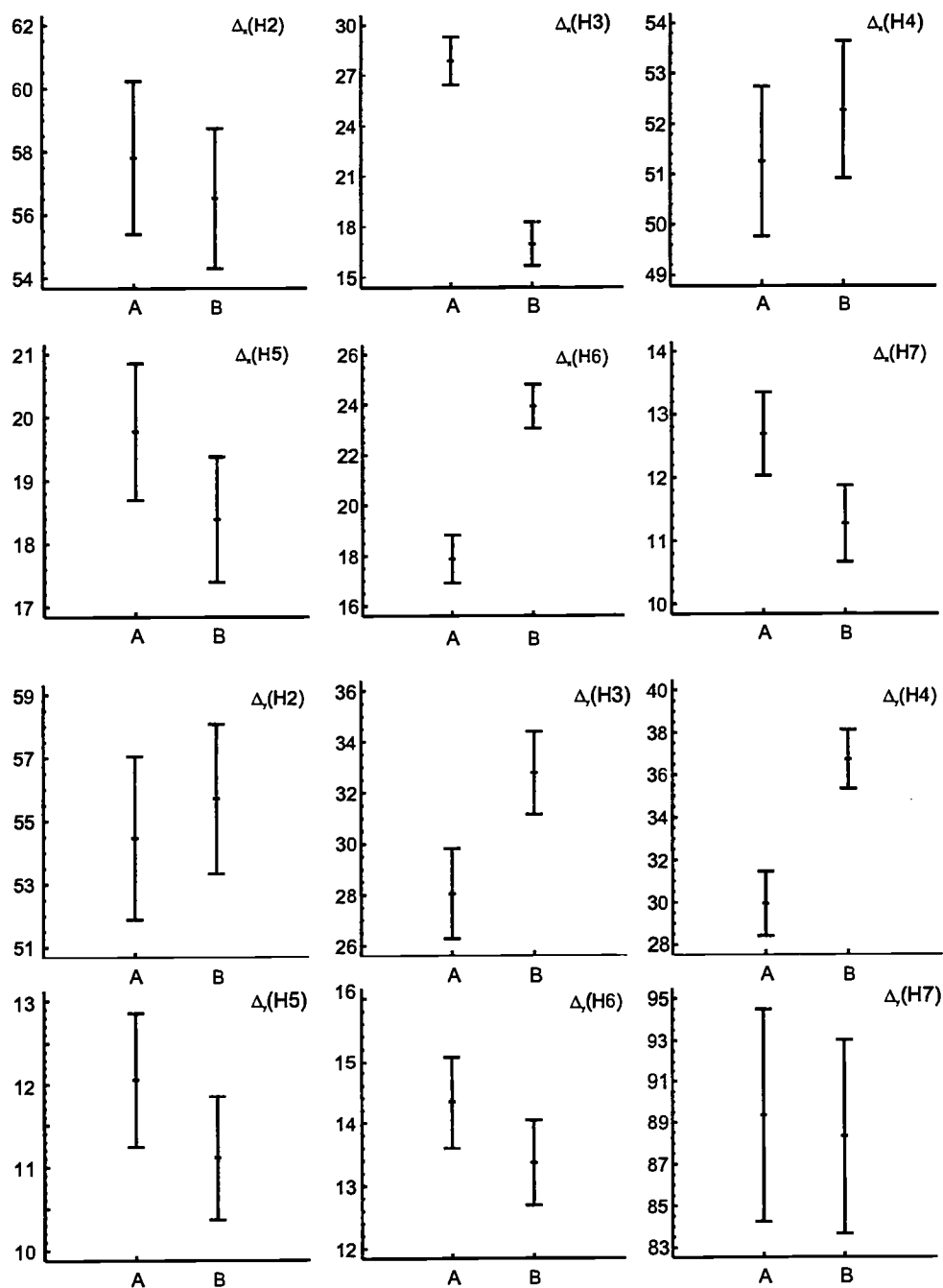
Figure 3.9. ANOVA mean plots and 95% Bonferroni confidence intervals of the condensed harmonic coefficient Δ_x and Δ_y for *Mylossoma aureum* lapillus shape types A and B, harmonics 2-7.

The DFA of the 24 informative harmonic coefficients showed that types (a) and (b) of *M. aureum* separated along the first axis (Fig. 3.10). *C. macropomum* and *P. brachipomus* were separated by the second (Fig. 3.10) and *M. duriventri* by the third canonical function (Fig. 3.10). Group discrimination was highly significant (Wilks Lambda= 0.072), with an overall classification efficiency of 89%. Only 31 of 273 otoliths were misclassified and most were misclassifications of the two *M. aureum* types (Table 3.4). Surprisingly, the two *M.aureum* types were more often misclassified as *M. duriventri* than as the other type of *M. aureum* (Table 3.4).

Table 3.4. Discriminant analysis classification of otolith shapes using Elliptic Fourier shape descriptors. (A) classification criteria for the two types of *M.aureum* based on hierarchical cluster analysis results (n=207), (B) visual shape classification of the two types of *M.aureum* based on a subset of randomly selected specimens (n=49).

Taxon	M.aureum (A)	M.aureum (B)	M.duri ventri	C.macrop omum	P.brachi pomus	Total	% correct
(A) Cluster based classification							
M. aureum (A)	81	2	11	0	1	95	85.2
M. aureum (B)	1	101	6	4	0	112	90.2
M. duriventri	1	2	30	0	0	33	90.1
C. macropomum	0	0	0	10	1	11	90.1
P. brachipomus	2	0	0	0	20	22	90.1
Total	85	105	47	4	22	273	
(B) Visual classification							
M.aureum (A)	16	4	1	0	0	21	76%
M.aureum (B)	1	24	2	1	0	28	85%
M. duriventri	0	1	32	0	0	33	96%
C. macropomum	0	0	0	10	1	11	90%
P. brachipomus	2	0	0	0	20	22	90%
Total	19	29	35	11	21	115	
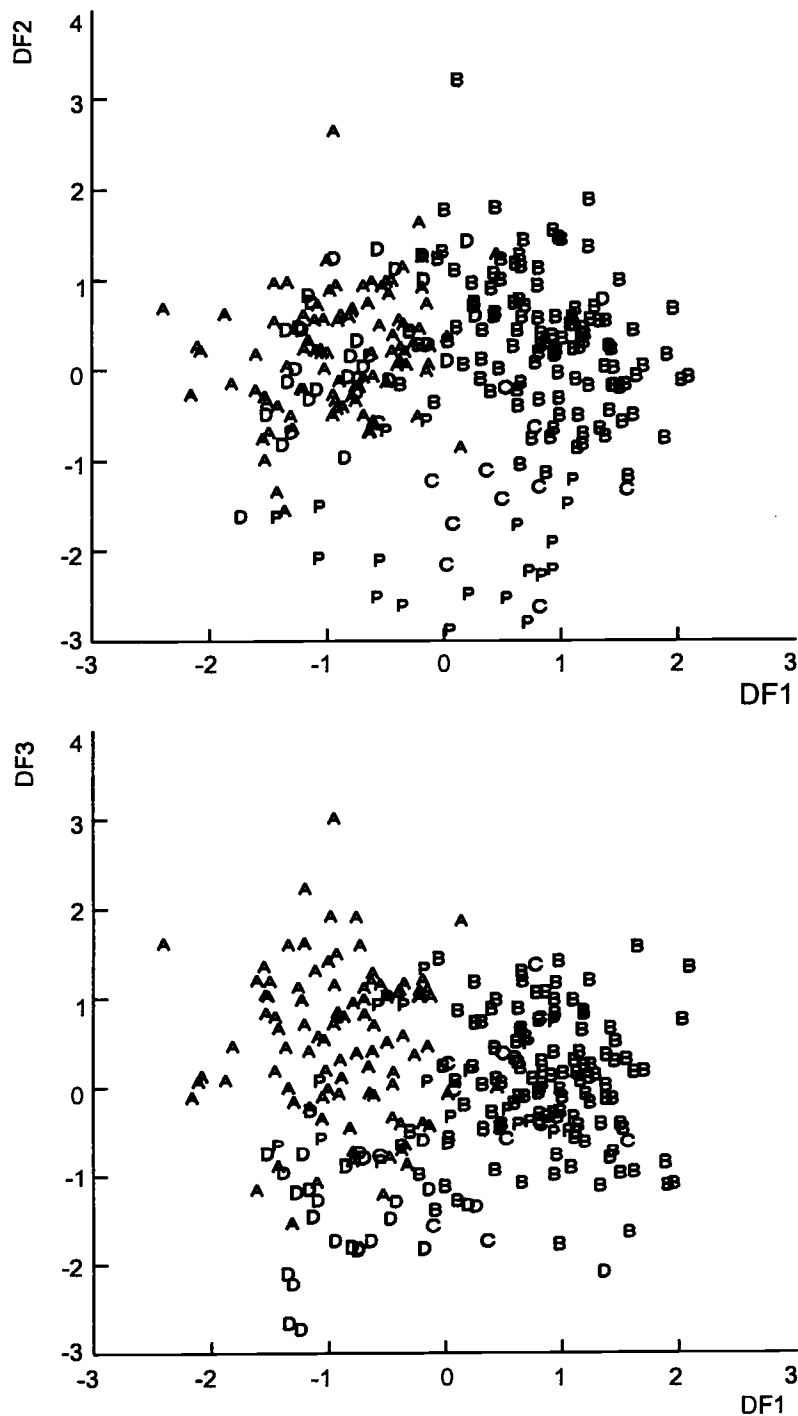
Figure 3.10. Plots of discriminant function scores for the lapillus shape analysis. (A) *Mylossoma aureum* type A, (B) *Mylossoma aureum* type B, (C) *Colossoma macropomum*, (D) *Mylossoma duriventri* and (P) *Piaractus brachipomus*.

Exploratory analyses of correlates to the two types of *M. aureum* did not detect ecological signals. There were no significant relationships between otolith type and otolith size, average microincrement width, fish size, fish age, or environmental variables at the time of capture (Table 3.5). Only dissolved oxygen had a weak relationship to PC1 (Table 3.5).

Validation of increment deposition rate

Fluorescent marks were more intense on lapilli and asteriscii than on sagittae. Both filter combinations produced similar fluorescent patterns, but the DAPI filter yielded better mark recognition when fluorescence intensity was low. Also, the blue fluorescence of the DAPI filter contrasted with otolith background color allowing simultaneous visualization of microincrements and fluorescent marks (Fig. 3.11).

Marking success and intensity of marks differed among the three marking techniques used (Table 3.6). Fish survival was 100% for all three marking treatments and there were no apparent signs of toxicity. Even fish subjected to intraperitonial injection resumed normal behavior immediately after treatment and fed normally within 12 Hs. Oral administration of OTC did not yield distinct recognizable marks on otoliths of the four fish treated. Fluorescent marks on otoliths treated by immersion and intraperitonial injection differed noticeably from auto-fluorescence.

Table 3.5. Pearson's correlations coefficients of principal components of shape coefficients, environmental variables and otolith attributes for 193 specimens of *M. aureum*. Variables are: water temperature (WT °C), Secchi disk (SEC), electric conductivity (EC), dissolved oxygen (DO), standard length (SL), age in days (age), average Microincrement width (INC), otolith length (OTLG), otolith anterior lobe length (ANTLG), otolith posterior lobe length (POSLG), Otolith area (OTAR) and otolith area vs. SL ratio (AR/SL).

	PC1	PC2	PC3	PC4	WT °C	SEC	H2S	EC	DO	SL	AGE	INC	OTLG	ANTLG	POSLG	OTAR
PC1	1															
PC2	0.064	1														
PC3	0.03	0.017	1													
PC4	-0.035	0.146	0.128	1												
WT °C	-0.055	0.006	0.041	0.084	1											
SEC	-0.158	0.146	0.149	-0.025	0.546	1										
H2S	0.224	0.227	-0.104	-0.076	0.206	0.344	1									
EC	-0.177	0.102	-0.039	-0.061	0.197	0.431	0.518	1								
DO	0.313	-0.092	-0.211	0.032	-0.066	-0.558	0.061	-0.308	1							
SL	0.261	0.067	-0.2	0.061	-0.048	-0.03	0.413	0.243	0.016	1						
AGE	0.041	0.053	-0.059	0.298	0.005	-0.052	0.054	-0.079	-0.095	0.564	1					
INC	-0.009	-0.191	-0.024	-0.056	-0.264	-0.259	-0.104	0.136	0.101	0.212	-0.291					
OTLG	0.205	0.001	-0.239	0.178	-0.073	-0.201	0.17	0.123	0.07	0.897	0.664	1				
ANTLG	0.015	-0.006	-0.026	0.24	-0.052	-0.096	0.147	0.043	-0.042	0.647	0.797	0.724	1			
POSLG	0.154	-0.058	-0.038	0.124	-0.049	-0.208	0.061	0.14	0.006	0.723	0.502	0.826	0.48	1		
OTAR	0.24	0.059	-0.24	0.141	-0.039	-0.181	0.244	0.139	0.078	0.907	0.67	0.962	0.725	0.812	1	
AR/SL	0.212	0.025	-0.241	0.184	-0.014	-0.285	0.073	0.028	0.133	0.708	0.646	0.891	0.678	0.782	0.935	0.927

Table 3.6. Oxytetracyclin treatments for otolith marking and microincrement deposition validation for *P. brachipomus*.

Treatment	Marker	N	Dosage	% mark retention	Mark quality
Injection	OTC HCl	24	150 mg/Kg	100	Excellent
Immersion	OTC Dih	16	600 mg/Kg	87.5	Variable
Oral	OTC Dih	4	150 mg/Kg	0	Absent

The immersion technique had 87.5% (n=16) mark retention. Fluorescent marks differed widely in intensity, ranging from weak and difficult to distinguish to intense and well defined. Marks also varied within otoliths among marking events (Fig. 3.11). All 24 fish treated with the injection technique (n= 15 for experiment 1 and n= 9 for experiment 2) had distinct, intense fluorescent marks. OTC uptake was restricted to one microincrement per marking event for both techniques although intense fluorescence from the injection technique gave the impression that marks extended to more than one increment.

Fish from immersion and intraperitonial injection treatments were combined into a single analysis. Relationships between observed number of increments and expected increments showed that increment deposition did not differ from a 1 to 1 ratio. The relationship between number of increments and time in days was: Days= 0.89 + 0.97 * number of increments, with df=25, R^2 =0.974, $SE_{intercept}$ =0.78 and SE_{slope} =0.03. Slopes were not significantly
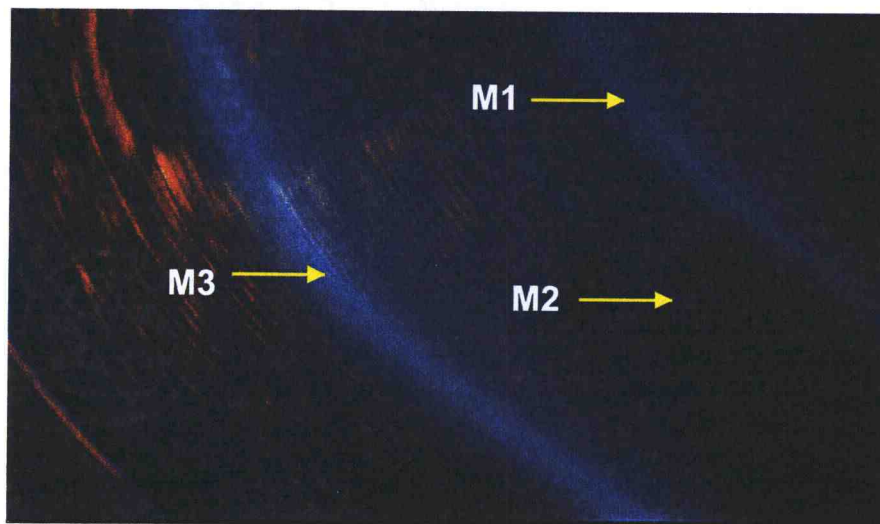
Figure 3.11. Sagittal section of the lapillus of *Piaractus brachipomus* showing OTC marks and microincrements. M1 and M2 were marks from immersion into OTC solution, M3 was from intraperitonial injection.
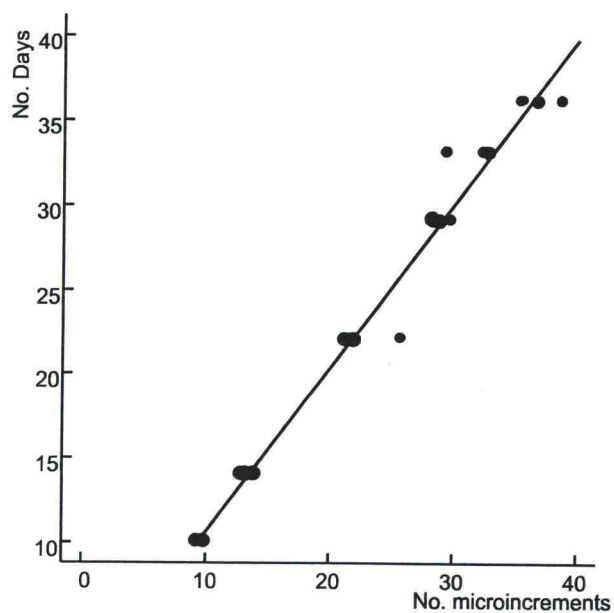

Figure 3.12. Linear regression plot of the relationship between number of observed microincrements and elapsed time in days for OTC marked lapillus of *Piaractus brachipomus*.

different from 1.0 ($t_{[25]}$ =0.911, p= 0.186) indicating increment deposition was daily (Fig. 3.12). Microincrement deposition pattern and rate did not differ before and after marking and no subdaily increments were observed. Precision of increment counts did not differ between marks created on different days or between a mark and the otolith edge. Differences between increments counts and days differed by an average of 4% (Range=0-10%), standard deviations averaged 0.96 (range=0-1.66). Changes in fish size were highly coupled to changes in otolith length in *P. brachipomus* (Table 3.7, Fig. 3.13), thus, otolith growth is a significant surrogate for somatic growth.

Table 3.7. Linear regression analysis for the relationship between somatic growth and lapillus growth for OTC marked *P. brachipomus*.

Anterior lobe growth vs. somatic growth					
Ind. Variable	Parameter	std. error	t-value	sig.level	
Intercept	-32.666	2.31	-14.13	.0000	
Slope	11.7815	.51	22.79	.0000	
Analysis of Variance					
Source	SS	DF	MS	F-Ratio	P-value
Model	5018.04	1	5018.04	519.7	.0000
Residuals	38.60	33	9.65		
Total (Corr.)	5336.64	34			
R-squared =	0.94				
Std.error est. =	3.10				
Posterior lobe growth vs. somatic growth					
Ind. Variable	Parameter	std. error	t-value	sig.level	
Intercept	-42.36	2.78	-15.20	.0000	
Slope	12.34	.55	22.40	.0000	
Analysis of Variance					
Source	SS	DF	MS	F-Ratio	P-value
Model	4957.16	1	4957.16	502.02	.0000
Residuals	315.97	32	9.87		
Total (Corr.)	5273.14	33			
R-squared =	0.94				
Std.error est. =	3.14				
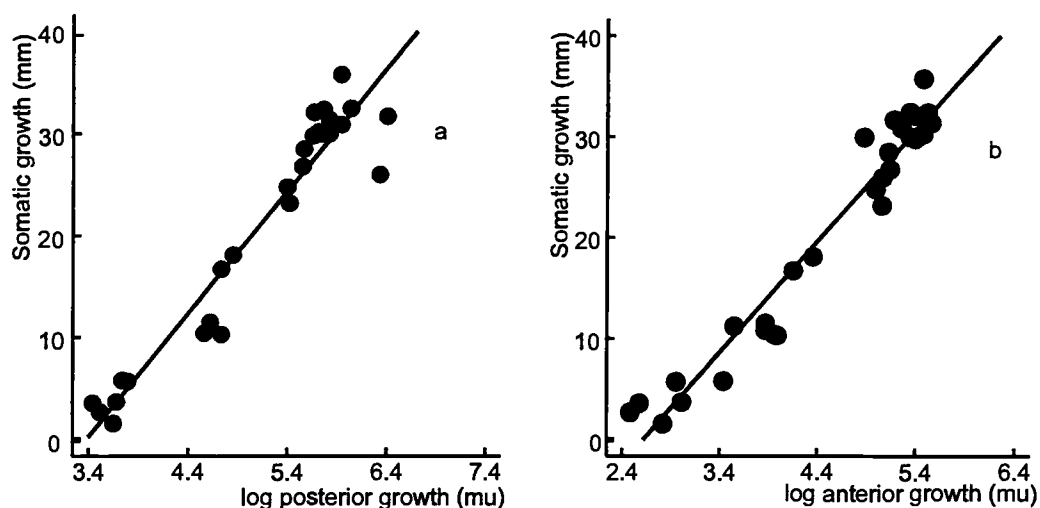
Figure 3.13. Log-Linear regression plots of the relationship between somatic growth and lapillus growth for OTC marked *Piaractus brachipomus*, (a)posterior lobe of lapillus and (b) anterior lobe of lapillus.

Discussion

Otolith development and microstructure

Asteriscii were poor otoliths for microincrement analysis because deposition was complex and results were inconsistent. Asteriscii in other ostariophysan fishes have produced similar results. Mugiya and Uchimura, (1989) noted asteriscii microincrements in goldfish were irregular and difficult to count and (Hoff et al., 1997) reported similar results in suckers. As in other ostariophysi (Frost, 1925; Adams, 1940; Weitzman, 1962; Rosen and Greenwood, 1970; Hoff et al., 1997)], the elongated morphology of the

sagittae and its allometric development (Fig. 3.1) produced a complex pattern of microincrements. Only cross sections could be produced and these were generally unsuitable for microincrement analysis. The lapillus was the only otolith in serrasalmins that was appropriate for microincrement analysis. Reduced allometric development (Fig. 3.1), consistent growth of the anterior lobe and the clear deposition of microincrements along this lobe (Fig. 3.3b) made the lapillus the preferred structure for microincrement analysis. Hoff et al., (1997) reached the same conclusion in studies of catostomid otoliths.

Shape analysis

Lapilli of the four species of serrasalmins analyzed in this study had an overall shape typical of characid fishes (Frost, 1925; Adams, 1940; Weitzman, 1962). Although relatively similar, lapilli shapes were species-specific (Fig. 3.6). Elliptical Fourier harmonic coefficients were sensitive to these differences and efficiently quantified shape variability within and among species (Table 3.1, Fig. 3.7). The absence of strong correlations between otolith length and otolith area with principal components scores (Table 3.5) indicated that standardized harmonic coefficients were indeed size invariant and extracted size independent pure shape information, allowing direct otolith shape comparison among specimens of different sizes.

The occurrence of distinct types of lapillus shapes within *M.aureum* (Figs. 3.5d, e and 3.8) was problematic. Two shape trajectories were

detected at all sizes above 25 mm SL suggesting shape dimorphism was not an ontogenetic artifact. Fish size, fish age, average microincrement width and growth rates did not have an effect on lapillus shape differences between the two types (Table 3.5). Similarly, otolith shape variability was not related to environmental conditions at the time of capture (Table 3.5).

The different types of *M. aureum* otoliths might be attributable to environmental factors (Campana and Casselman, 1993) such as parasites, early growth rates, or oxygen deficiency. Slow-growing heavily parasitized fish had thicker and wider otoliths when compared to less parasitized fish (Gauldie et al., in press). Shape patterns have been shown to be dependent on growth rates during larval and early juvenile stages (Secor and Dean, 1989). Slow growth during larval period can change concavity and thickness and distort sagittal profiles (Lagardère et al., 1995). Campana and Casselman, (1993) found that growth rates have a larger influence on otolith shape than geographic origin, age, gender or year-class. Growth related geographic differences in otolith shape were also suggested for *Etelis carbunculus* (Smith, 1992). In the Amazon floodplain oxygen deficiency is a very common event in areas inhabited by *M. aureum*. (Mugiya and Takahashi, 1985) reported that calcium mobilization from otoliths was caused by respiratory acidosis. Extended hypoxic conditions induced calcium remobilization in goldfish otoliths, resulting in the formation of distinct checks in otoliths (Mugiya and Uchimura, 1989). Chronic exposure to hypoxic

conditions could trigger physiological changes that could result in calcium resorption from the otoliths and contribute to changes in otolith shape.

The different types of *M. aureum* otoliths might be attributable to genetic factors (Gauldie et al., in press) such as sexual dimorphism or species differences. Sexual dimorphism in otolith shape was reported for haplochromin cichlids but the proximal cause of differences may have been growth related with fast growing males having more elongate, thinner otoliths (Gaemers and Crapon de Crapona, 1986). Bird et al., (1986) and (Castonguay et al., 1991) did not find any otolith shape differences that could be attributes to sexual dimorphism, indicating that although it might be present in some species, it is not universal. The pattern of lapillus shape variability in the four species and two types of *M.aureum* (Fig. 3.10 and Table 3. 4) might indicate the presence of two cryptic species.

Both genetic and environmental factors seem likely explanations for the two types of otoliths in *M.* aureum. Of the environmental factors, growth rate and oxygen deficiency seem most probable. Because it is generally not possible to know the habitat-use history of a wild-caught fish, only controlled experiments can address the question. Of the genetic factors, two cryptic species seems the most likely. The absence of otolith dimorphism in closely related species suggests that sexual dimorphism is less likely. I could not find meristic or morphometric differences among fish represented by the two otolith shape types (unpublished data).

Cryptic species would be expected to be very similar, so the absence of differences does rule out their possibility.

Validation of increment deposition rate

The effectiveness of marking otoliths with OTC depended on method of treatment. Oral administration of OTC failed. Immersion in OTC solution (87.5% mark retention) and intraperitonial injection (100% mark retention) were effective. As in other studies, OTC oxidized during immersion treatment, turning from yellow to brown, but oxidation did not seem to influence fish behavior or OTC assimilation (Schmitt, 1984) and (Thomas et al., 1995). The positive results using immersion in 500 mg/l of OTC for 24 hr were congruent with prior studies (Schmitt, 1984; Tsukamoto, 1988; Tzeng, 1989; Hendricks, 1991; Thomas, 1995). But, (Brooks et al., 1994) showed that shorter-term exposure at 500 mg/l of OTC also resulted in high percentages of marked fish. Immersion reduces handling and mutilation and has been recommended for larvae and young juveniles (Thomas et al., 1995). Intraperitonial injection is rapid and highly reliable with OTC incorporation in 50% of the specimens after 10 hr and 100% after 24 hr (Campana and Nielson, 1982). Problems include tissue damage, swelling and skin discoloration (Marking et al., 1988), dosage-related mortality (McFarlane and Beamish, 1987), poorly defined increments (Toole et al., 1993), and retention causing multiple increment marking and

diffuse fluorescence (Toole et al., 1993; Thomas et al., 1995). Only the latter

problem was observed in this study (Fig. 3.11).

The marking experiments in juvenile *P. brachipomus* showed that

lapillus microincrements are formed daily (Fig. 3.12). Microincrement

formation has been showed to be daily in many marine and freshwater non-

ostariophysan teleosts (Geffen, 1992), but only a few ostariophysans (Tzeng

and Yu, 1989; Mugiya and Tanaka, 1992; Hoff et al., 1997). The confirmation

of daily microincrement formation in lapilli of *P.brachipomus* increases the

probability that other Amazon ostariophysi have daily deposition. Although

validation is typically recommended for each species of study, the diversity of

Amazon ostariophysi and the need to better understand general patterns of

recruitment in Amazon floodplain fishes makes such a recommendation

impractical. As a first order approximation, lapillus microincrements appear to

be a reliable estimator of daily age and an important tool for studies of

recruitment processes of Amazon ostariophysans.

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Chapter 4

Distribution, Growth and Mortality of Early Life History Stages of *Mylossoma aureum* in the Amazon Floodplain

Abstract

Patterns of spatial distribution, growth and mortality characteristics of larvae and juvenile were examined for *M. aureum* inhabiting the floodplain of the Amazon river in the vicinity of Manaus. Otolith-derived birth date reconstruction showed that *M.aureum* 's spawning season extended from late November to March, and that peak larvae recruitment occurred in mid-December. Larvae and juveniles had different spatial distribution in relation to habitat usage. Instantaneous growth coefficients(g) varied from 0.0197 d^{-1} to 0.265 d^{-1} among cohorts. Early-season cohorts had wider otolith microincrements and higher instantaneous growth coefficients than late-season cohorts. Mortality was estimated by the decline of $\log_e$ (abundance) regressed on age, and results indicated that cohort-specific mortality varied significantly among cohorts, ranging from 0.027 (2.6%/d) to 0.103 (9.7%/d). Recruitment potential (proportion of fish surviving to 65 days) was shown to be higher for mid-season cohorts than for early or late-season cohorts.

Introduction

Large tropical rivers have pronounced fluctuations in water level associated with seasonal flood pulses and extensive floodplains. The flood pulse produces a constant shift in availability of habitats that make up the river-floodplain complex (Welcomme, 1979). In the Amazon, the flood pulse dramatically affects the landscape and has been shown to be a crucial link in the dynamics of the system (Junk et al., 1989). Many species of fishes take advantage of the flood pulse and spend part of their life cycle in floodplain habitats (Goulding, 1980; Junk, 1984; Junk et al., 1997).

Many migratory fishes in the Amazon synchronize spawning with the onset of the flooding season and spawn in the main channel (Araujo-Lima, 1984; Petry, 1989; Fernandes, 1997; Araujo-Lima and Oliveira, 1998; Oliveira and Araujo-Lima, 1998). Because main channel productivity is very low, food supply for larval fishes is not adequate (Fisher, 1979; Forsberg et al., 1988), making the channel a poor nursery habitat. Nevertheless, Many larval characiform are known to drift down the channel prior the onset of exogenous feeding (Araujo-Lima, 1984; Petry, 1989; Oliveira and Araujo-Lima, 1998; Leite and Araujo-Lima, in press). Araujo-Lima (1994) showed that characiforms hatch in about 12 hr, have a short larval stage, and starvation occurs from 6 to 10 days after hatching if exogenous feeding does not occur. Synchronizing spawning with the onset of rising water would increase the probability of larval transport into the floodplain (Petry, 1989), where survival

chances are higher than in the main channel (Araujo-Lima and Oliveira, 1998). Floodplain lakes have been suggested as the most important nursery habitat for migratory characiformes (Schwassmann, 1978; Saint-Paul and Bayley, 1979; Goulding, 1980), but little is known about biotic and abiotic mechanisms that affect larval and juvenile recruitment to them.

It is widely believed that early life stages play an important role in determining year-class strength (Crecco et al., 1983) and that changes in mortality rates during larval stages have a profound impact on population size. In recent years several studies have indicated that changes in mortality rates during early juvenile stages may play a bigger role than previously assumed in determining year class strength (Sissenwine, 1984; Houde, 1987; Campana, 1996). Thus, understanding processes that regulate mortality during the juvenile stage can help to answer to questions related to recruitment variability and population growth rates (Sogard, 1997).

Otolith microstructure analysis has provided the means to estimate age and growth rates at the individual level, and to determine birthdate frequencies of cohort survivors. Combining population age structure with abundance-at-age relationships can be used to estimate cohort-specific mortality rates. Therefore, otolith-derived demographic parameters may be used to determine causes and consequences of differential survival (Rooker et al., 1999).

In this study I analyze the spatial and temporal use of an Amazon floodplain island by larval and juvenile *Mylossoma aureum*. Otolith microincrement analysis was used to characterize the temporal distribution of birth dates and its relation to hydrologic conditions. The spatial and temporal effects on growth rates and mortality estimates for several cohorts of the 1993 year-class were also investigated for the main nursery vegetation type (*Paspalum repens*).

Methods

Field collection

Newly recruited larvae and juveniles of *M. aureum* were collected from Marchantaria Island, Solimões River near Manaus, Brazil during the initial phase of the annual flooding season. Sampling was carried out every two weeks between January and April 1993 (139 samples collected during seven sampling trips). All collections were made with a 25X6 m seine net with 5 mm mesh size, following the method described in (Bayley, 1983). Samples were taken from five geographic areas at the island and seven strata defined by the aquatic macrophytes: *Echinochloa polystachya* (canarana=CAN), *Paspalum repens* (membeca=MEM), and *Panicum sp* (PAN) *Eichhornia crassipes* (EIC) and *Pistia stratiotes* (PIS), *Paspalum fasciculatum* (murim=MUR) and open water free of vegetation (UNV) (Petry, 2000, chapter 2).

Specimens were preserved in 70% ethanol immediately after capture and standard length (SL) measured to the nearest 0.1 mm without adjustments due to shrinkage. Catchability corrected densities estimates were obtained for each sample by correcting raw catches with the appropriate size dependent gear efficiency correction derived from a calibration procedure conducted in the same area (Bayley and Herendeen, in press).

The aquatic environment increases dramatically in area during the flood, thus requiring fish abundance estimates to be based on fish densities during each sampling period. Synthetic aperture radar (SAR) imagery obtained from JERS-1 NASDA satellite was used to estimate changes in area of aquatic macrophytes coverage during each sampling period. Images from four dates and four different water levels (Jan. 28 1995 at 21.87m, Feb. 23 1993 at 24.41 m, Feb. 10 1994 at 25.03 m and May 09 1994 at 27.87 m) were used. The February 23, 1993 image was used as the reference image to co-assign remaining images and calculate areas of interest. Full resolution 12 m pixels were degraded to 25 m resolution to reduce speckling and then classified into: open water areas, flooded macrophytes, flooded forested areas and unflooded areas.

Abundance of larvae and juvenile *M. aureum*, 12-45 mm SL, were estimated for each sampling interval from fish density (=catch/catchability per m^2 sampled) estimated for each sample and using those estimates to estimate abundance accounting to current total area of flooded macrophytes. Because

67% of *M. aureum* juveniles catch occurred in stands of *Paspalum repens* (membeca), and all size classes were well represented in this vegetation type during the entire sampling period, abundance estimates were restricted to this macrophyte samples, and its proportion to the total area of flooded macrophytes was estimated to be 9% at each of the 7 sampling intervals. Therefore, subsequent mortality estimates based on abundances reflect the conditions for membeca stands only. The Fish size limits were based on inspection of the size frequency distribution. Net selectivity rather than recruitment to the island appeared to be partially responsible for incomplete sampling of specimens below 12 mm SL because of low catchability, (Bayley and Herendeen, in press). At sizes classes greater than 45 mm SL, catches were too low to reliably estimate abundance and mortality.

Otolith analysis

Lapillar otolith microstructure was used to estimate individual age and growth of larvae and juvenile *M. aureum* (Petry, 2000, chapter 3). Five specimens were randomly selected for each mm size class (12 - 45 mm SL) from each sampling interval (when available) and otoliths removed. A total of 559 lapillar otoliths were removed and processed following Petry (2000, chapter 3). Increment deposition rate has not been validated for this species, but was assumed to be on a daily basis, Petry (2000 chapter 3). Increment counts and increment widths were obtained under light microscopy with the

aid of Optimas 5.0 image analysis system using a magnification of 200 to 400x, along a straight line from the primordium to the anterior edge of the lapillus. Age distributions in the population were estimated based on the proportion represented by each mm size class. Birthdates were determined by subtracting the increment count from the date of capture. Birthdates were used to assign each specimen into one of 7 successive 10-day cohorts. Seven cohorts were identified numerically as follows: Nov. 27- Dec. 06 (1); Dec. 07-16 (2); Dec. 17-26 (3); Dec. 27- Jan. 05 (4); Jan. 06-15 (5); Jan. 16-25 (6) and Jan. 26 – Feb 08 (7).

Estimates of initial growth rates (first 20 days) were used to evaluate variability in growth rates among sampling areas, vegetation types and cohorts. Mean width of the first 20 increments was used as an index of initial growth. Cohort-specific daily instantaneous growth coefficients were calculated from the exponential model described as:

$$Log_e(L_t)= Log_e(L_0) -gt,$$

Where L_t = length (mm SL) at time t;
L_0 = estimated fish length at hatching
g = instantaneous growth coefficient (/d);
and
t = otolith-derived age in days.

Instantaneous growth coefficients (g) for each of the 559 fish aged was estimated using otolith-derived estimates of age and assuming a hatching length (L_0) of 4 mm SL for all cohorts. The growth coefficient was then calculated as $g=Log_e(L_t/L_0)/t$. Because this coefficient has a strong size

component, it was regressed on SL to remove the size effect and the residuals were then used to compare individual growth characteristics among cohorts.

Cohort-specific instantaneous mortality rates were estimated by regression of $\log_e$ (abundance) on age, where abundance was estimated as catchability and area corrected catches, and age was otolith-derived age in days. Each survey gave up to 10 abundance at age estimates for each cohort. The exponential model of decline was used to calculate instantaneous mortality rates as follows:

$$Log_e(N_t) = Log_e(N_0) - Mt,$$

Where N_t = abundance at time t;
    N_0 = estimated abundance at time t_0
    M = mortality;
    and
    t = time elapsed between t and t_0.

Abundance at age was used instead of mean age of cohorts per survey because means integrate mortality over the 10 d cohort interval effectively overweighting the abundance of younger fish on the estimated mortality rate. Each birthdate group within a cohort could only be sampled once at each age, which gives a biologically more meaningful summary of mortality. Stage-specific mortality rates (47 days between 19 and 65 days of age) were also estimated for each cohort as $-M = Log_e (N_t/N_0)$. These habitat-based mortality estimates were based on two assumptions: 1) individuals recruiting to

membeca stands would remain in the habitat for the entire period for which mortality rates were estimated; and 2) immigration and emigration from other areas or habitats were negligible. There is strong evidence that larvae and young juveniles of Mylossoma only use macrophyte stands as nursery and are not found in the river channel, flooded forest or pelagic zone of floodplain lakes (Leite and Araujo-Lima, in press), thus supporting the first assumption. Failing to account for the effect of immigration or emigration on abundance estimates can be an important source of bias in mortality estimates (Frederick, 1997). Nevertheless, the absence of pronounced increases or decreases in densities of length groups over time, which would be expected if emigration or immigration took place, suggests that the second assumption has not been strongly violated.

Data analysis

An exponential model regressing macrophyte area on river stage level was used to estimate changes in aquatic macrophytes area during the flood. Analysis of variance (ANOVA) was used to examine the effect of vegetation types and sampling areas on density of larvae and juveniles *M. aureum*. Density estimates were log-transformed to minimize heteroscedasticity. ANOVA was also used to test for temporal and inter-cohort differences in mean otolith- increment width, and inter-cohort differences for instantaneous growth coefficients based on individual fish. Analysis of covariance

(ANCOVA) was used to test for inter-cohort differences in growth and mortality estimates. An interaction regression model was fitted to test for regression slope differences (homogeneity of slopes assumption; (Zar, 1984).

Results

Estimates of flooded areas

Area covered by aquatic macrophytes (y) at Marchantaria Island was estimated by: *y= 4.209 + 4.385*ln(stage-21)* (Table 4.1, Fig. 4.1). Area of aquatic macrophytes changed from 3.55 km^2 at river stage 21.87 m to 12.47 km^2 at river stage 27.87 (Fig. 4.2).

Table 4.1. Regression analysis of the relationship between river stage at Manaus harbor and area of aquatic macrophytes flooded at Marchantaria Island. Estimates derived from JERS-1 25 meter resolution images.

Ind. Variable	coefficient	std. error	t-value	sig.level
Constant	4.209	0.334	0.13E+02	0.006
LGAUG_21	4.385	0.249	0.18E+02	0.003

(*LGAUG_21= natural log of river stage – 21*)

Analysis of Variance

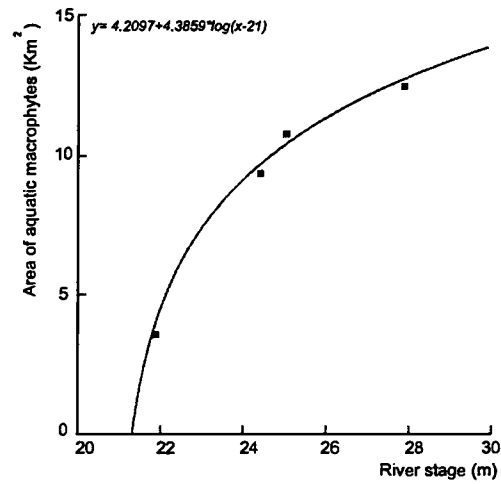| Source	SS	DF	MS	F-Ratio	P-value
Model	44.672	1	44.672	308.82	0.003
Error	0.289	2	0.144		
Total (Corr.)					
R-squared =	0.994				
St.error est. =	0.380				
R-squared (Adj. for d.f.) = 0.990					

Figure 4.1. Fitted model for the relationship between river stage at Manaus harbor and flooded aquatic macrophytes area at Marchantaria Island during the rising limb of the hydrograph. Derived from JERS-1/NASDA, SAR Images.
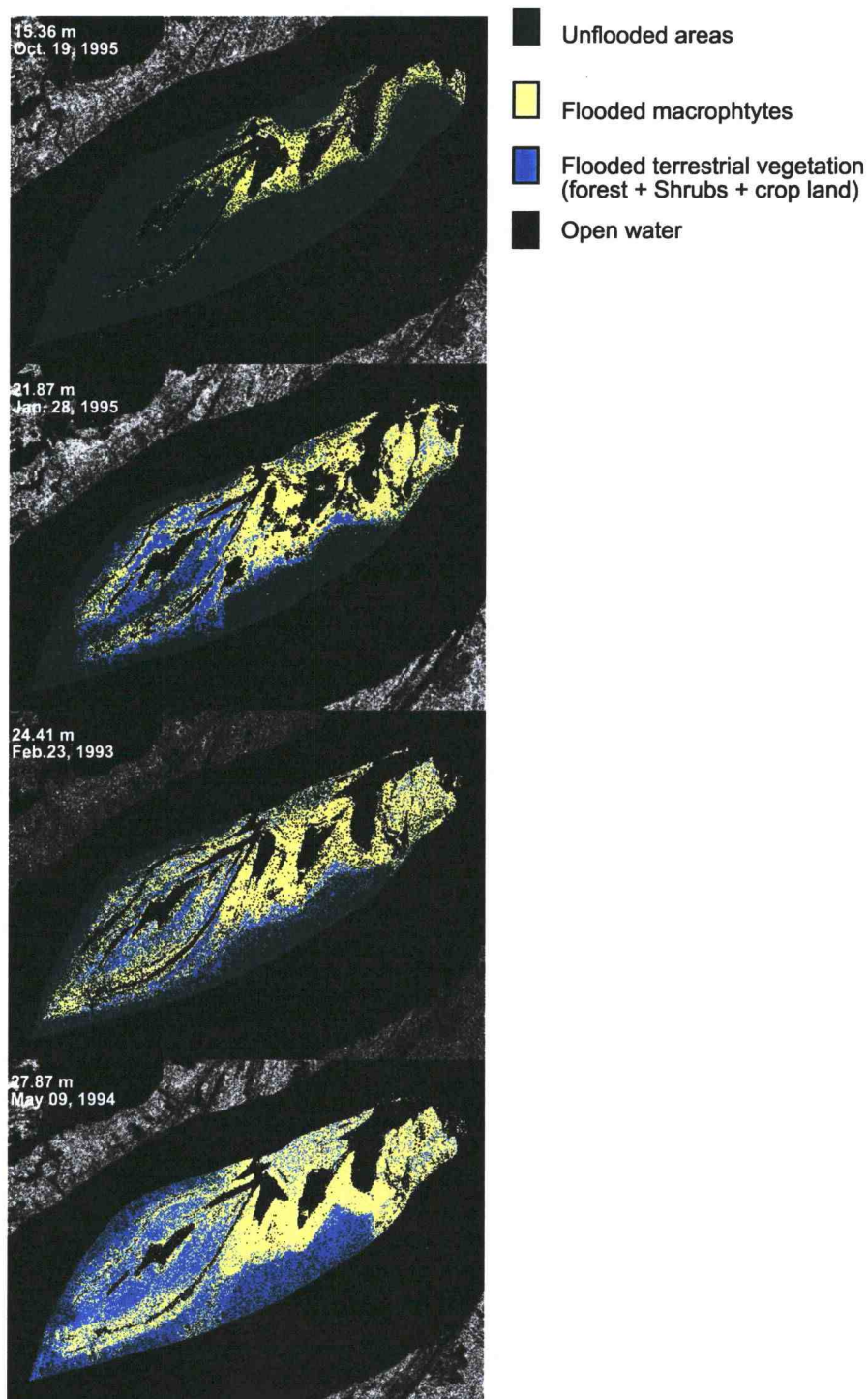
Figure 4.2. Classification of JERS-1\NASDA SAR images (25m pixels) of the progression of flooding at four river stages during the rising limb of the hydrograph. Flooding sequence of Marchantaria Island, reference image Feb.23 1993 at 24.41 m river stage.

Catch composition characteristics

A total of 2653 larvae and juveniles of *M. aureum,* 9-71 mm SL, were collected from 126 samples at Marchantaria Island between January 4 and April 1, 1993. Larvae, 11-15 mm SL, were the most abundant sizes, and larvae below 11 mm SL were underrepresented presumably because of low catchability due to size selectivity of the gear (Fig. 4.3). There were 928 larvae, 9-16 mm SL, from 82 samples; 1237 small juveniles, 17-35 mm SL, from 105 samples, and 486 large juveniles, >35 mm SL, from 77 samples.
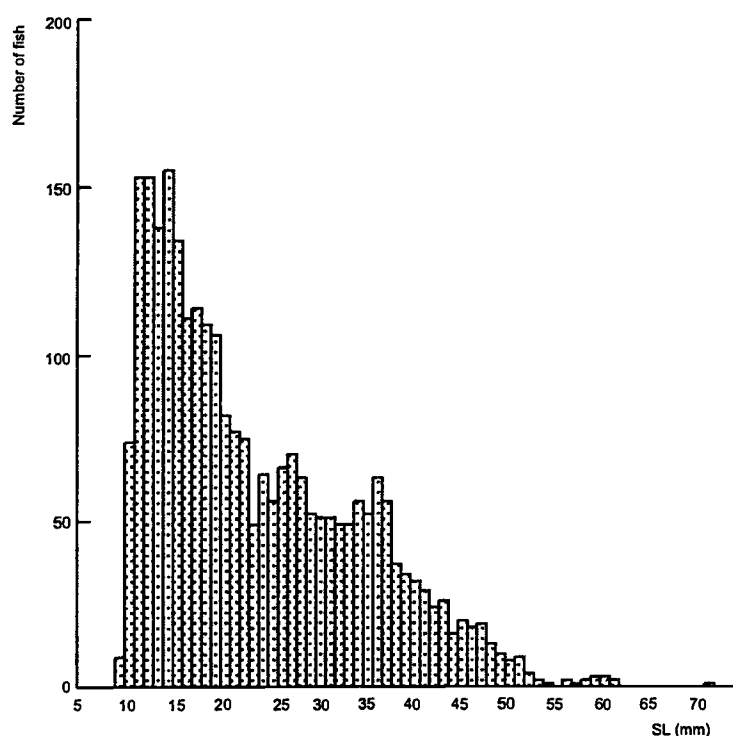

Figure 4.3. Length-frequency composition of *Mylossoma aureum* catch from Marchantaria Island during the 1993 flooding season between Jan. 04 and Apr. 01 (n=2653).

Catchability corrected densities varied from 0.0 to 1263/50m^2 for larvae, 0.0 to 151.35/ 50m^2 for small juveniles and from 0.0 to 30.74/50m^2 for large juveniles. Larvae were present during the entire sampling period, but were caught in higher densities between January 5-21. Larger juveniles were more abundant from mid-February to the end of March.

Spatial distribution

Densities of larvae and juveniles *Mylossoma aureum* were compared among the five geographic sampling areas and vegetation types. Larvae tended to be more concentrated close to the river in shallow areas, whereas juveniles tended to be distributed in deeper water further inside the floodplain (Fig. 4.4). Larval densities were significantly higher in area 1 (close to the river) than at area 5 (farthest from river) (F=3.37, p=0.01), but were not statistically different among the remaining areas (Fig. 4.5a). Larval densities per sample were significantly higher (F=3.36, p=0.004) in membeca and *Pistia* stands than in unvegetated areas (Fig. 4.5b). Densities of small juveniles did not differ significantly among sampling areas(F=1.32, p=0.26), nevertheless a decline from area 1 to area 5 was observed (Fig. 4.6a). Small juveniles were significantly denser at membeca sites (F=11.17, p<0.0001) than for all other vegetation types and unvegetated sites, with the exception of murim sites (Fig. 4.6b). Large juveniles densities did not differ significantly among the 5

sampling areas (F=0.62, p=0.65) (Fig. 4.7a), but were significantly denser in

membeca sites (F=7.87, p<0.0001) than at any other vegetation type or
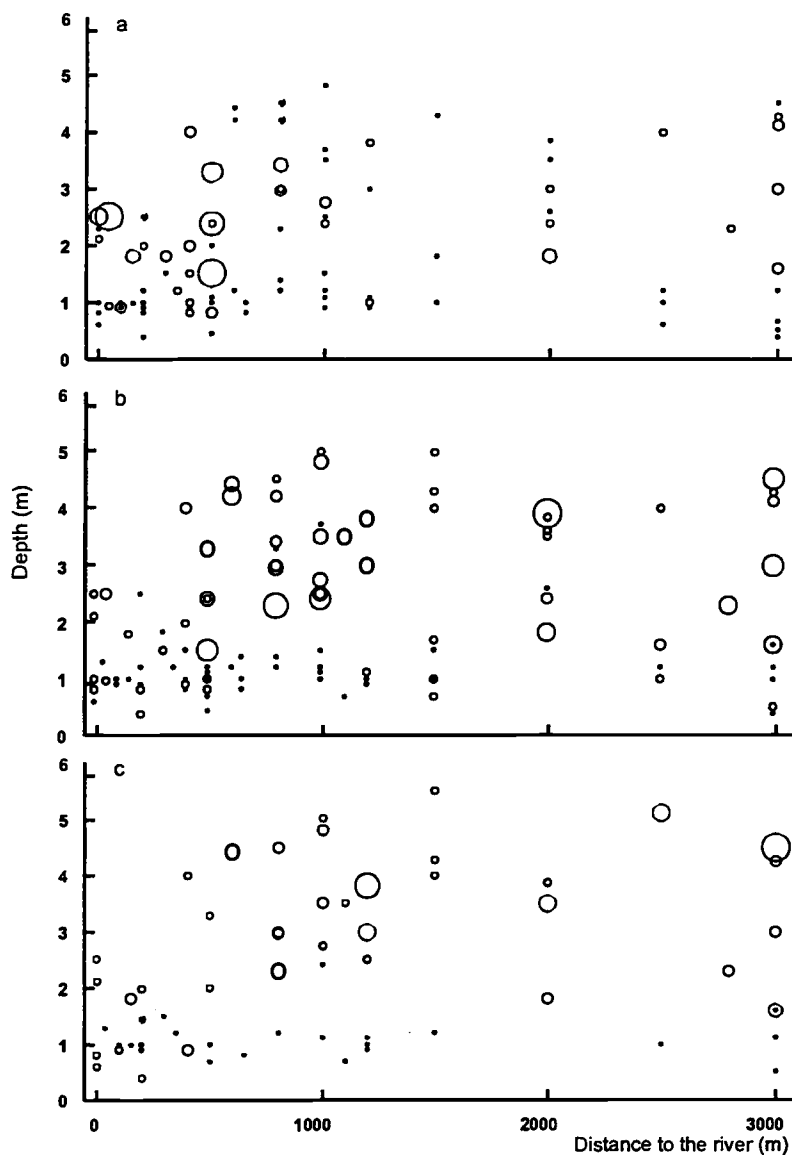
unvegetated sites (Fig. 4.7b).

Figure 4.4. Spatial distribution of *Mylossoma aureum* in relation to water depth and distance to the river. Larvae (12-16 mm SL) (a), young juveniles (17-35 mm SL) (b) and large juveniles above 35 mm SL(c). Diameter of

circles is proportional to catchability corrected densities. Zero densities are represented by dots.

Figure 4.5. ANOVA means and 95% Bonferroni confidence interval plots for larval *Mylossoma aureum* (12-16 mm SL) distribution in relation to geographic sampling areas (a) and vegetation types (b). Areas are: (A1) Southeastern shallows, (A2) Bay in front of Lake Camaleão, (A3) Northeastern shallows, (A4) Bottom of lower bay and (A5) Lake Camaleão. Vegetation types are: (Can) canarana, (Eic) *Eichhornia*, (Mem) membeca, (Mur) murim, (Pan) *Panicum*, (Pis) *Pistia* and (Unv) unvegetated).
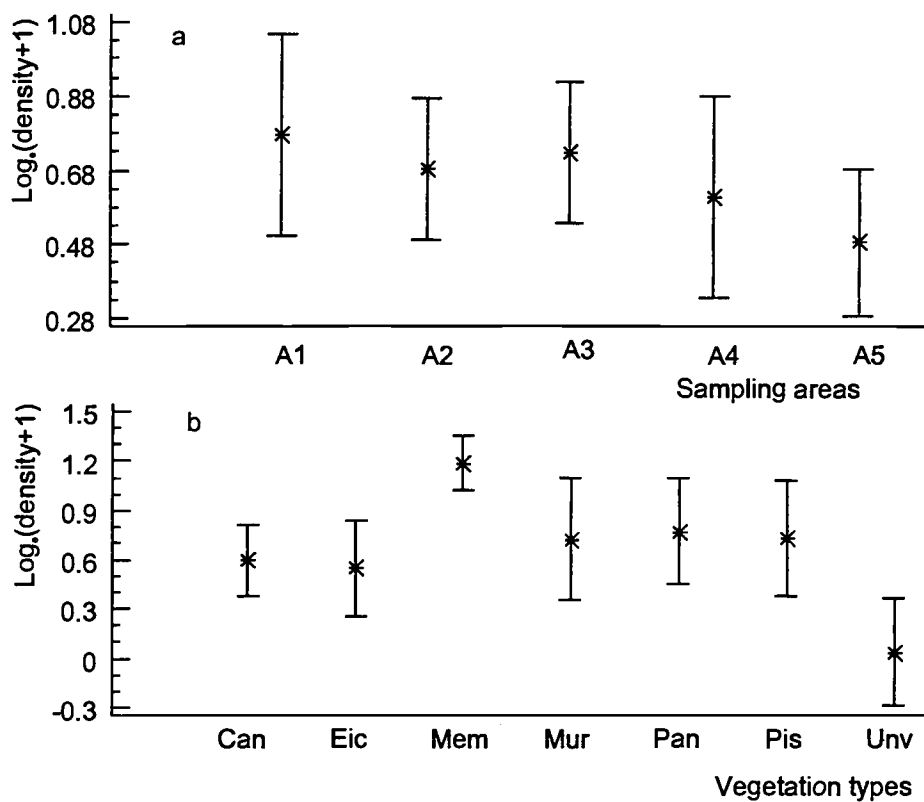
Figure 4.6. ANOVA means and 95% Bonferroni confidence interval plots for *Mylossoma aureum* small juveniles (17-34 mm SL) distribution in relation to geographic sampling areas (a) and vegetation types (b). Areas are: (A1) Southeastern shallows, (A2) Bay in front of Lake Camaleão, (A3) Northeastern shallows, (A4) Bottom of lower bay and (A5) Lake Camaleão. Vegetation types are: (Can) canarana, (Eic) *Eichhornia*, (Mem) membeca, (Mur) murim, (Pan) *Panicum*, (Pis) *Pistia* and (Unv) unvegetated).
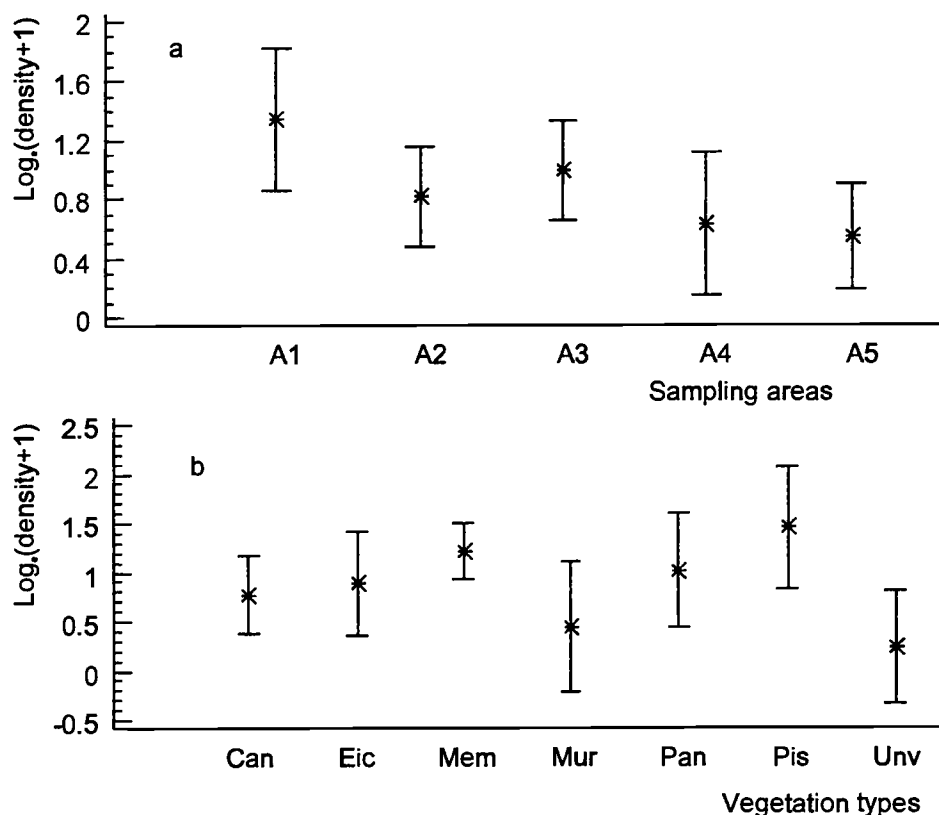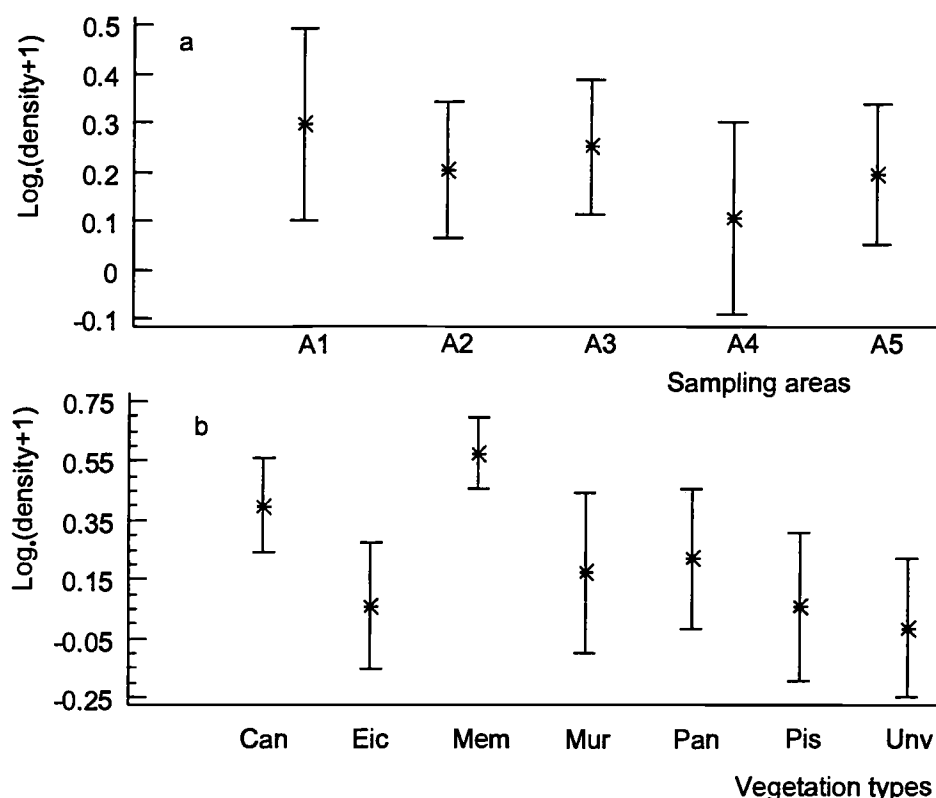
Figure 4.7. ANOVA means and 95% Bonferroni confidence interval plots for *Mylossoma aureum* large juveniles (35-45 mm SL) distribution in relation to geographic sampling areas (a) and vegetation types (b). Areas are: (A1) Southeastern shallows, (A2) Bay in front of Lake Camaleão, (A3) Northeastern shallows, (A4) Bottom of lower bay and (A5) Lake Camaleão. Vegetation types are: (Can) canarana, (Eic) *Eichhornia*, (Mem) membeca, (Mur) murim, (Pan) *Panicum*, (Pis) *Pistia* and (Unv) unvegetated).

Birth date distribution

Birth distribution of *M. aureum* was obtained from otolith-derived ages (increment counts) from 559 specimens. Size-at-age per mm size class was used to estimate age distributions of un-aged fish. Abundance estimates per birth date were adjusted for catchability and based on total area

of habitat. Birth date distribution ranged over 126 days, from Nov. 4, 1992 to

Mar. 6 1993, although most fish were born within a 92-day period, from Dec. 1

to Mar. 3 (Fig. 4.8). Abundance per birth date was strongly related to daily

flooding rates (R^2 =0.45, p<0.0001) (Fig. 4.9). Peak abundances occurred

between flood days 31 and 48, Dec. 11-28, coinciding with the highest daily

flooding rates (> 0.10 m/d) for the rising limb of the hydrograph. Modal

birthdate was estimated to be on December 15 (river stage 19.94, flood day
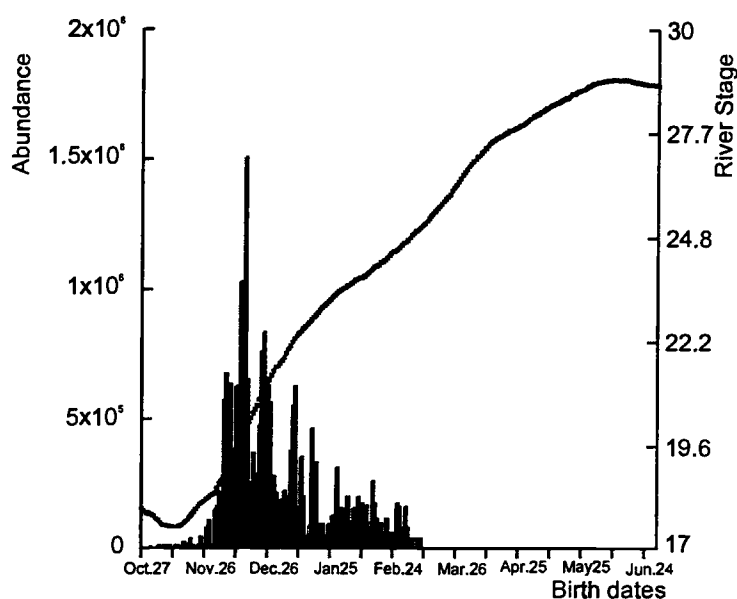
35).

Figure 4.8. Frequency histogram of birth distribution of *Mylossoma aureum* in relation to water level changes during the rising limb of the hydrograph for the Amazon flooding season of 1993 at Marchantaria Island. River stages from Manaus Harbor.
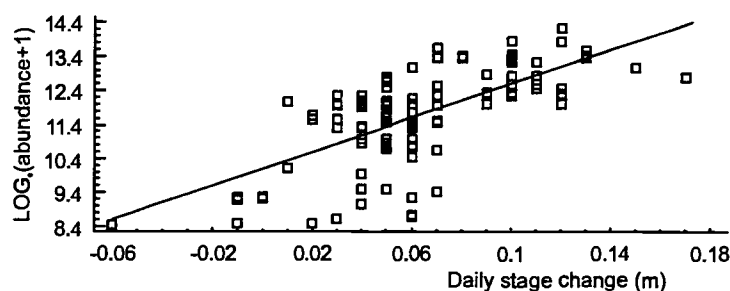
Figure 4.9. Regression plot of the relationship between abundances per birth date and daily river stage change at Manaus harbor for the period between Oct.27,1992 and Mar 03, 1993.

Cohort-specific growth

Cohort-specific instantaneous growth coefficients (g) for the seven 10-day cohorts of *M. aureum* were estimated for the first 65 days of age, and ranged from 0.020 to 0.0265 d^{-1}. A comparison of slopes of log$_e$ (SL) on age by cohort, showed a significant cohort effect (ANCOVA, different slopes, $F=2.99$, $p=0.007$). Estimated cohort-specific instantaneous growth rates based on the regression model tended to be higher for later cohorts. There was no clear temporal pattern, growth coefficients increasing between cohort 1 and 3, declining to the lowest value for cohort 4 and increasing between cohorts 5 and 7 (Table 4.2, Fig. 4.10).

Mean otolith increment width for the first 20 increments did not differ significantly between sampling dates within cohorts, examples of the pattern

are shown in (Fig. 4.11) for cohorts 1, 3 and 6. Early cohorts showed a slight

tendency for increment width reduction over time (Fig. 4.11a), mid-season

cohorts initially increased then decreased over time (Fig. 4.11b), and late-

season cohorts tended to increase over time (Fig. 4.11c). Mean increment

widths for the first 20 increments pooled across all sampling dates showed a

significant effect among cohorts (ANOVA, F=4.98, p=0.0001). Early-season

cohorts had wider increment widths than late-season cohorts (Table 4.2, Fig.

4.11d). No significant effect of vegetation type on mean increment was found

(Fig. 4.11e).

Individual fish instantaneous growth coefficients adjusted for fish size

were not significantly different among sampling areas (ANOVA, F= 0.82,

p=0.5151) (Fig. 4.12a). Instantaneous growth coefficients were significantly

different among vegetation types (ANOVA, F=5.92, p< 0.0001), *Pistia* had

higher mean values than membeca and murim (Fig. 4.12b). There was also a

highly significant cohorts effect (ANOVA, F= 6.46, p< 0.0001) (Fig. 4.12c).

Fish from early-season cohorts had mean instantaneous growth coefficients

higher than late-season cohorts, consistent with the pattern observed for

mean increment widths for the first 20 days. Mean fish size at 65 days of age

was not significantly different among cohorts (ANOVA, F=1.65, p=0.15),

although mean size declined from early-season cohorts to late-season cohorts

(Table 4.2).

Table 4.2. Growth and mortality coefficients for *Mylossoma aureum* juveniles 10-day cohorts. Estimates given are :cohort-specific instantaneous growth coefficient , mean otolith increment width for the first 20 increments, mean size independent residual instantaneous growth, mean fish size at age 65 days, instantaneous mortality coefficients, stage-specific mortality estimates between the age of 19 and 65 days and recruitment potential (surviving fish to 65 days of age). *Estimates for cohort 1 were based on reduced time interval (33 to 65 days) because of incomplete catch of cohort 1.*

Cohort	Cohort g (d⁻¹)	Mean Inc. width	Mean g residual. per fish *10⁴	SL at age 65 days	M (d⁻¹)	mortality for 47 days (19-65)	Rec. potential %
Coh1	0.020	5.03	20.8	35.0	-0.056 (5.4%/d)	-	4.6
Coh2	0.022	5.03	20.7	34.0	-0.103 (9.7%/d)	5.1 (99.4%)	8.2
Coh3	0.023	4.97	12.6	32.0	-0.068 (6.5%/d)	3.3 (96.3%)	18.0
Coh4	0.019	4.90	-2.7	32.5	-0.027 (2.6%/d)	1.2 (72.3%)	36.8
Coh5	0.022	4.89	2.1	33.1	-0.054 (5.2%/d)	2.6 (92.6%)	15.9
Coh6	0.026	4.77	-17.1	30.5	-0.027 (2.6%/d)	1.2 (72.3%)	5.4
Coh7	0.024	4.54	-14.5	31.3	-0.046 (4.5%/d)	2.2 (89.0%)	10.8
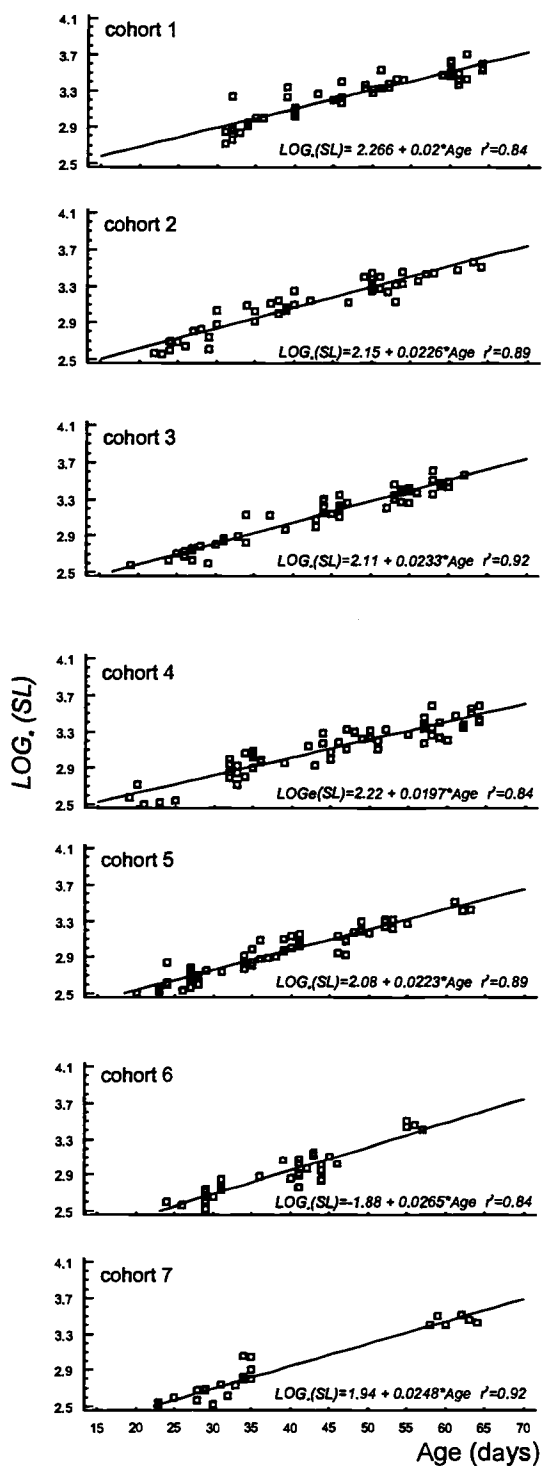
Figure 4.10. Size-at-age relationship for each ten-days cohorts for the age interval between 19 and 65 days of age, based on otolith-derived age estimates. Linear model equations given for each cohort.
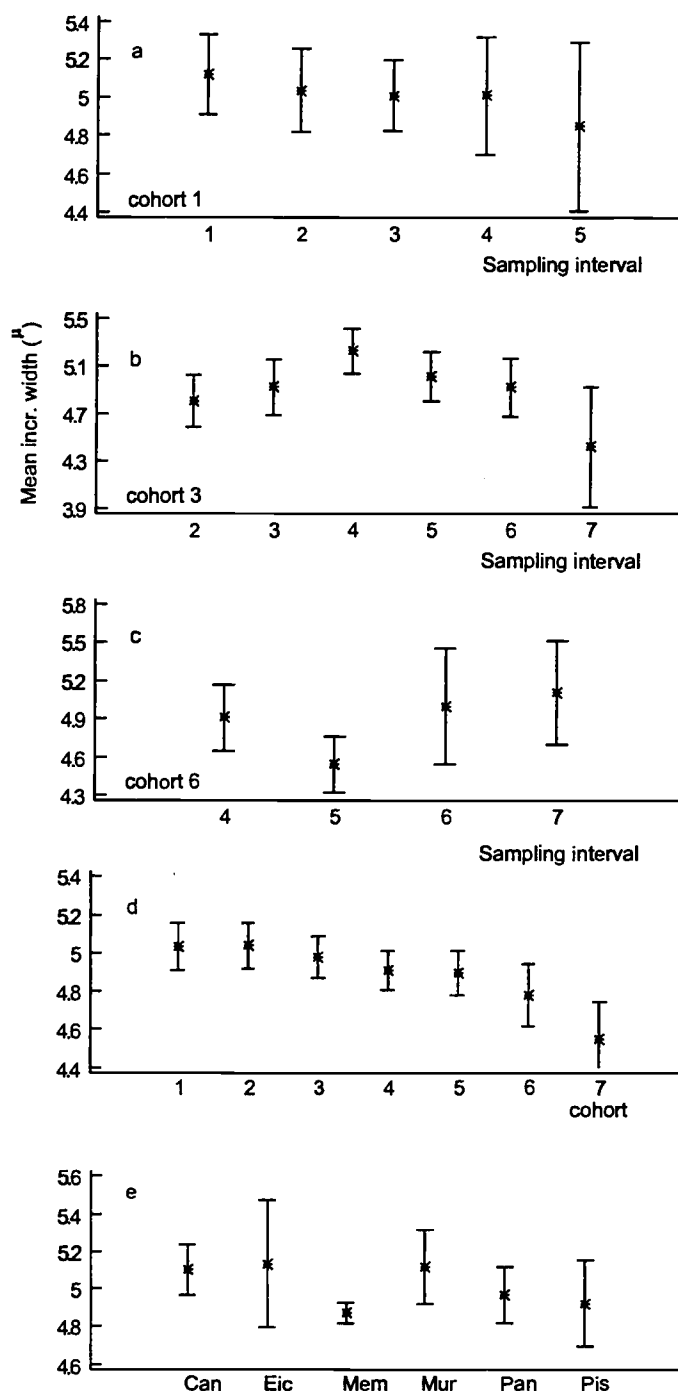
Figure 4.11. ANOVA mean plots and 95% Bonferroni confidence intervals for the temporal effect of otolith increment width variation for the first 20 increments (a-c). Effect of cohort on otolith increment width (d) and effect of vegetation types on mean otolith increment width (e). Sampling intervals are the sequential 2 weeks time intervals.
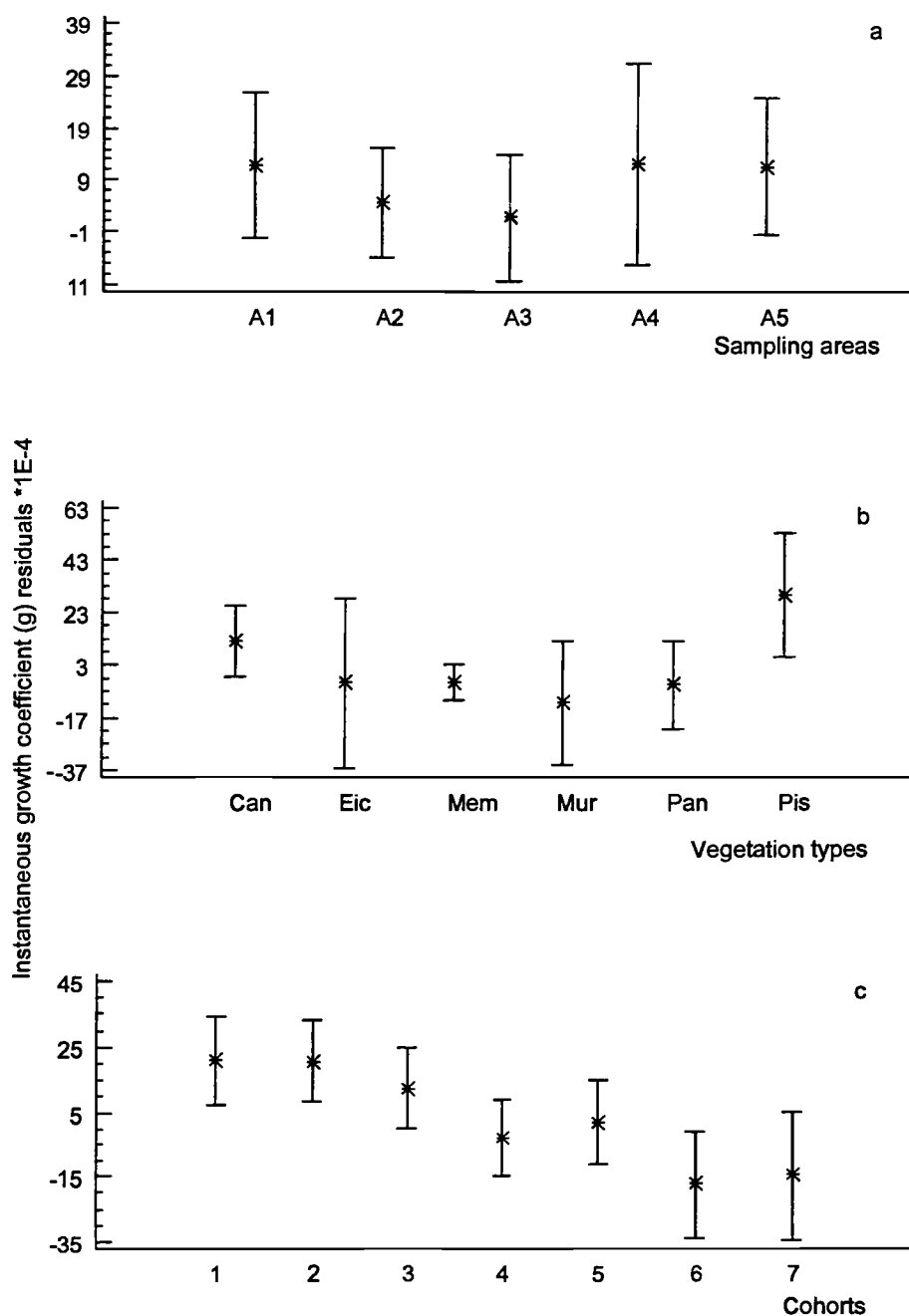
Figure 4.12. ANOVA means plots and Bonferroni 95% confidence intervals for size independent instantaneous growth coefficient $g(d^{-1})$ residuals for 19-65 days old. By vegetation types (Can) canarana, (Eic) *Eichhornia*, (Mem) membeca, (Mur) murim, (Pan) *Panicum* and (Pis) *Pistia*) all cohorts combined (a); by sampling areas, all cohorts combined (b); and by individual cohorts, all data pooled (c).

<u>Mortality estimates</u>

Instantaneous mortality coefficients (*M*) estimated for the for the seven 10-day cohorts from age 19 to 65 days were estimated exclusively for membeca samples. Coefficients ranged from 0.027 (2.6%/d) to 0.103 (9.7%/d), and a significant difference was detected among cohorts (ANCOVA, slopes, F=6.54, p< 0.0001) (Fig. 4.13). Mortality rates were higher for early-season cohorts (1, 2 and 3) and lower for late-season cohorts (6 and 7). Although mortality rates for cohort 1 were in the range estimated for the other cohorts, its value cannot be compared directly to the remaining cohorts because of incomplete catch. When sampled for the first time, members of cohort 1 were older than fish from later cohorts, thus potentially subestimating mortality. Mortality between ages of 19 and 65 days showed that cohort 2 suffered the highest accumulated mortality with a decline in abundance of 99.3% from the beginning of the period. Cohorts 4 and 6 had the lowest accumulated mortality, with 72.3% for the same time frame (Table 4.2). Estimates of recruitment potential per cohort (total contribution of each cohort to the year-class for fishes that survived to age 65 days) showed that mid-season cohorts 3, 4 and 5, that were 42.3% of the fish at age 19 days, contributed with 70.7 to the fishes that survived to 65 days. Cohorts 1 and 2, which had 49% of the initial numbers, contributed with 12.8% at age 65 days, and cohorts 6 and 7, which were 7.9% initially, contributed with 16.2% (Table 4.2).
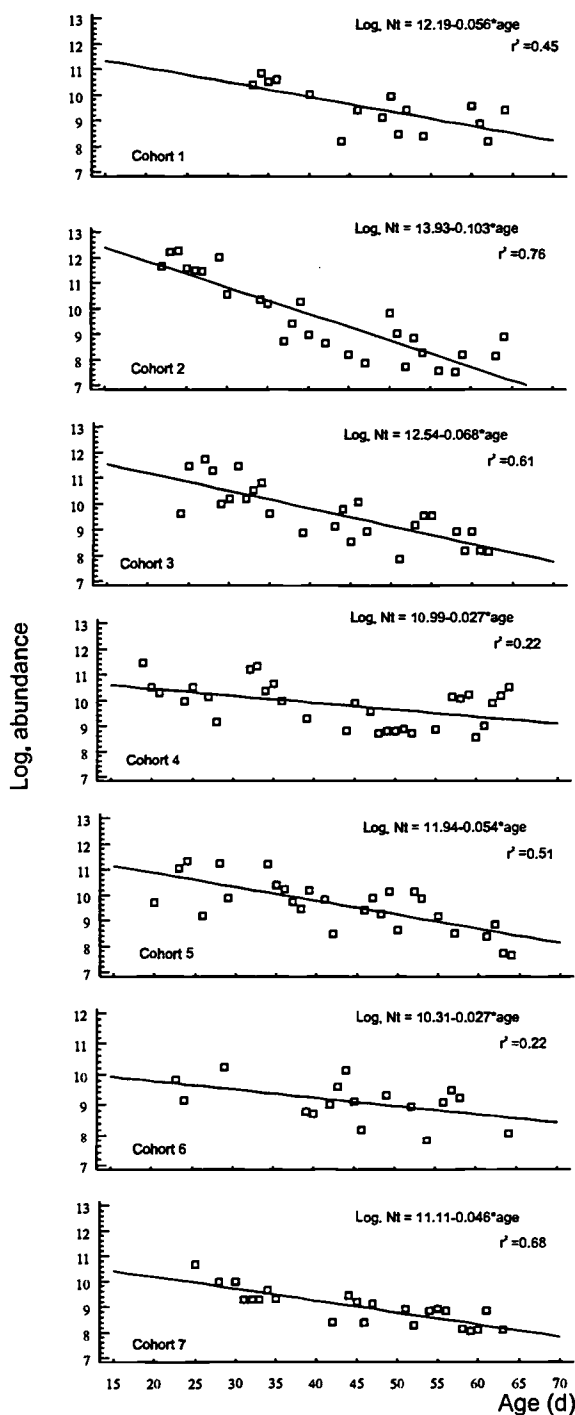
Figure 4.13. Regression plots of Log_e(abundance) on age for the 10-day cohorts of larvae and juvenile Mylossoma aureum collected from Marchantaria Island between Jan-Apr. 1993. Regression equations and plots are shown for all cohorts from 1-7.

Discussion

The density of larvae recruiting into the floodplain was significantly higher in sampling area 1 (closest to the main channel) than in area 5 (~2.5- 3 km farthest inside the floodplain) (Fig. 4.5a). These results indicate that as soon as larvae reach the floodplain they colonize suitable nursery habitats at the edges of the floodplain in contact with the main channel. *Mylossoma* larvae drifting down the main channel have a heterogeneous spatial distribution, being more concentrated along the riverbank and at the mouth of floodplain lakes than in the center of the main channel (Oliveira and Araujo-Lima, 1998). This pattern was also found for several other species of floodplain dwelling characiforms and attributed to hydrodynamic processes associated with spawning and larval behavior (Araujo-Lima and Oliveira , 1998). Only young pre-flexion *M. aureum* larvae below 7 mm SL were found to be drifting in the main channel and none had passed the first feeding stage after yolk absobtion (Oliveira and Araujo-Lima, 1998; Leite and Araujo-Lima, in press). These studies indicate that larvae do not complete metamorphosis through first feeding in the river channel and require nursery habitats in the floodplain to survive. Leite and Araujo-Lima (in press) showed that *M. aureum* larvae did not stay in open water after reaching the floodplain and did not use the flooded forest as a nursery. They also showed that only larvae collected in aquatic macrophytes had started exogenous feeding, which suggests that aquatic macrophytes are the main nursery habitat for this species.

The current study showed that there was not a strong selectivity by the larvae to any particular type of macrophyte as nursery habitat when recruiting to the floodplain. Nonetheless, *Pistia* and membeca has slightly higher mean densities than the other macrophytes (canarana, *Eichhornia*, murim and *Panicum*), and both *Pistia* and membeca had significant higher densities than unvegetated areas (Fig. 4.5b). Similar results were obtained by (Leite and Araujo-Lima, in press), who reported larvae association with membeca roots.

Juvenile *M. aureum* did not show significant spatial distribution differences (Fig. 4.6a and 4.7a) among the 5 sampling areas. Because larvae are more abundant in area 1 (Fig. 4.5a), this indicates that as fish grow, they either disperse deeper into the floodplain (Fig. 4.4) or experience greater mortality closer to the river. Larval and small juvenile densities are about equal in area 5 (Figs. 4.5a and 4.6a) suggesting no mortality, an unlikely possibility. Thus, growing fish probably disperse deeper into the floodplain as the water rises. Small juveniles had significantly higher densities in membeca stands than in any other macrophyte type (Fig. 4.6b). Because larval and small juvenile densities in membeca are about equal (Figs. 4.5b and 4.6b), fish in this habitat either experienced no mortality or this vegetation type was actively selected. Membeca probably provides better predator protection than most other habitats but since zero mortality is unlikely, habitat selection is presumed to drive this pattern, and some immigration could be taking place. Developing juvenile *M. aureum*, therefore appear to move deeper into the

floodplain and preferentially select membeca stands.

Birth date frequencies from otolith-derived age estimates indicate that the spawning period of *M. aureum* is highly coupled with the river's hydrological regime (Fig. 4.8). Peak spawning during the 1992-1993 flooding season occurred between December 1, 1992 and January 3, 1993 when flooding rates surpassed 10 cm/d. Spawning continued until the beginning of March. The temporal distribution of larvae drifting down the main channel in 1981-82, 1984-85 and 1994-95 was from December through April (Oliveira, 1996) and corroborates these results. The synchrony of spawning and flood hydrographs in the Amazon is due to the constraint of characiform early life history. Larvae hatch 12-16 hr after fertilization and starvation can occur 6-10 days later if exogenous feeding is not started (Araujo-Lima, 1994). Because of this small window of opportunity for larvae to reach nursery grounds inside the floodplain, many species have synchronized spawning with the onset of the flood cycle. There is also evidence that mean peak spawning varies among species at different times during the flood increase (Bayley, 1983; Oliveira, 1996). Spawning while flood rates are high would increase chances that larvae would be transported into floodplain lakes (Petry, 1989), thus increasing the probability of survival. The coupling of birthdates and flood hydrograph (Fig. 4.8) and the work of Araujo-Lima and collaborators strongly suggest that an accelerating rise in water level during the onset of the flooding season is the most important environmental cue to trigger fish spawning along

the Amazon main channel.

Extension of the spawning season beyond the initial rise may negate uncertainties of the early hydrologic regime. Short-term, unpredictable flood retreats are not uncommon during the early phase of the flooding season (Petry 2000, chapter 1). These retreats drain water from recently flooded areas, forcing larvae to remain in the channel where starvation could decimate a year class. By extending reproductive effort over a longer time frame, a species could compensate for these early unfavorable hydrologic conditions.

Most analyses indicated that early season cohorts grew faster than later cohorts, but sample sizes were smaller for cohorts 6 and 7, 20-22 vs. 38-47 for cohorts 1-5. Conversely, the first twenty increments of early-season cohorts were significantly wider than those of late-season cohorts, especially cohorts 6 and 7 (Fig. 4.11d). Within a cohort, the mean increment width did not change significantly during the season (Fig. 4.11 a, b, c), indicating that later survivors were not a biased sub-sample of the population at age 20 d. Size independent instantaneous growth coefficients also declined during the season and again were lowest in cohorts 6 and 7 (Fig. 4.12c). Size-at-age relationships showed a different pattern with cohorts 6 and 7 having significantly higher growth coefficients (Fig. 4.10).

Vegetation type also had an effect on increment width, suggesting that habitat characteristics as well as birthdate could have influenced individual growth patterns (Fig. 4.11e). Vegetation types had a significant effect on size

independent instantaneous growth coefficients (Fig. 4.12b) with canarana and *Pistia* having higher rates and membeca having an average rate. Although membeca had higher average fish densities, the fish did not have higher in this habitat. Membeca was also the macrophyte type with the highest total species packing (Petry, 2000 chapter 2) suggesting that high density did not severely reduce growth. Others have also been unable to detect relationships between density and growth in freshwater fishes (Bayley, 1988) (Kapetsky, 1974) (Rutherford et al., 1995). (Bayley, 1988) hypothesized that flooding increased food supply concurrently with increasing recruitment and that growth was partially modulated by oxygen. I could not find any significant effect of oxygen on growth. Others have shown that oxygen concentrations could be involved in habitat selection (Junk et al., 1983; Soares, 1993) and I have suggested that all studies have inadequately partitioned the influences of oxygen and vegetation type (Petry, 2000 chapter 2). Habitat selection in *M.aurem* clearly involves a trade-off between growth and predation risk with preferences for habitat type and oxygen concentration more closely related to predation risk (Petry, 2000 chapter 2) than to growth.

Instantaneous mortality rates of young *M.aureum* were high and variable among cohorts (Table 4.2). Cohorts 4 and 6 had the lowest mortality rates, both were 72.4%, while mortality rates for other cohorts were 89.1-99.4% (Table 4.2). Overall 12% of the initially recruited larvae reached an age of 65 days. Mortality rates were not coupled to initial abundance. Cohort

2, for example, had the highest initial abundance but its high mortality rate reduced its contribution to the population of 65 day-old fish to only 8.2% (Table 4.2). Cohorts 3 and 4 contributed more than 50% to the population of 65 day-old fish, indicating that earlier and later cohorts had lower recruitment potential in 1992-1993.

Although high mortality rates are known to be common among larval fishes (Rooker et al., 1999; Houde, 1987; Houde, 1996; Houde, 1997) very little is known about mortality rates in juvenile stages especially in tropical rivers. (Hoggarth and Halls, 1997) showed that total survivorship between years was only 1-4%, and consequently stocks were mainly comprised of fish less than one year old. A similar pattern was reported for the Amazon floodplain (Bayley, 1983). The estimate of 12% survivorship during the 47 day period between age 19 d and 65 d in *M. aureum* suggests that this narrow time frame may be one of the most important in determining total survivorship. Because the 1992-1993 flooding season was ideal with the river rising at a steady rate throughout the period (Fig. 4.8), above the mean rising regime for the period (Petry, 2000 chapter 1), the 12% estimate of survivorship may be higher than in years with a more complex hydrologic regime. Nevertheless, my mortality estimates might be underestimated due to the potential effect of immigration of juveniles from other vegetation types to membeca stands. Clearly, survivorship in *M. aureum* had temporal and spatial components in 1992-1993. The current study suggests that predation risk drives recruitment

processes in *M. aureum* but only long-term sampling allowing for inter-annual comparisons will resolve the details.

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Chapter 5

Conclusions

This study has shown that fish assemblages in the Amazon River floodplain are strongly structured along well-defined environmental gradients, mainly formed by dissolved oxygen concentrations and aquatic vegetation characteristics, during the flooding season. I presented evidences that there is a strong relationship between fish species diversity, distribution and abundance, with the composition of emergent aquatic macrophytes in the floodplain. These findings support the hypothesis that fish assemblages strongly respond to abiotic conditions of the environment, as well as to biotic interactions (predominantly predation pressure) during the flooding season, similar to what has been reported for other large tropical river systems during the dry season (Tejerina-Garro et al., 1998; Rodriguez and Lewis, 1997). My results contrast with prior assertions that fish communities are loosely organized in the Amazon and that species associations are unpatterned because of environmental variability related to the flood pulse (Goulding et al., 1988; Lowe-MacConnell, 1975).

This work corroborates the hypothesis that the floodplains have an important role in the life cycle of numerous species of fish and that these

areas are critical for the survival of young of the year recruits, as it has been suggested for many large tropical rivers with pronounced seasonal flooding regime (Lowe-MacConnell, 1964; Welcomme, 1979; Bayley, 1988; Machado-Allison, 1987; Machado-Allison, 1990).

My data suggest that variability in the hydrological conditions may be a strong modulators to determine the strength of recruitment and consequently for fish production. Despite that my observations were collected during a year of almost ideal hydrological conditions, a noticeable temporal variation in mortality rates was observed. In years of unfavorable hydrologic conditions, with prolonged flood retreats, it is likely that mortality rates of recruiting juveniles would be much higher than those estimated by me, and could result in significant recruitment failures. The analysis of the historical hydrologic records from Manaus showed that flood retreats during the recruitment season are a common event in central Amazonia (Petry, 2000 Chapter 1), nonetheless very little attention has been given to their impact on fish recruitment in the floodplain. To access the impact of the hydrologic regime on fish recruitment in the Amazon floodplain system, a long term study with multiple years of observations is fundamental.

Although my dataset was geographically constrained to a specific area of the Amazon floodplain, the findings reported herein most likely apply to other areas in the floodplain to a certain degree. In this context, it is imperative that larger empirical datasets with broader geographic scope need

to be acquired to test the validity of my results in a more comprehensive approach

The rapid increase of human populations along the Amazon main channel, the increase in fishing pressure and substantial alteration of the floodplain environment by new land use practices, such as cattle and buffalo ranching, may cause severe impact in fish stocks. Special attention should be directed to analyze the effects of aquatic macrophytes removal from the floodplain and its consequences to fish production. Knowledge of the processes that influence fish population dynamics in the floodplain are of crucial importance to establish coherent guidelines for effective management of fisheries resources in the Amazon floodplain and to make effective fish biodiversity conservation decisions.

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