Ecomorphological correlates of thirteen dominant fish species of Amazonian floodplain lakes.

FREITAS[1]; C.E.C.;   COSTA[1], E.L. & SOARES[3], M.G.M.

[1] Departamento de Ciências Pesqueiras / Faculdade de Ciências Agrárias.Universidade Federal do Amazonas. Av. Gen. Rodrigo Otávio, 3000. 69077-000.Manaus – Amazonas –rasil.cefreitas@ufam.edu.br

[3] Instituto Nacional de Pesquisas da Amazônia. Caixa Postal, 478, 69011-090. Manaus - Amazonas, Brasil, 643-3269. gesoares@inpa.gov.br

ABSTRACT: Ecomorphological correlates of thirteen dominant fish species of Amazonian floodplain lakes. Ecomorphological attributes of thirteen fish species of Amazonian floodplain lakes were estimated and related then to the feeding habits. Relationship between feeding habits and the morphology for thirteen species belongs to Serrasalmidae and Cichlidae Families were identified. A strong relationship between morphology and the feeding habits, was verified but that morphology also can be an important predictor of the habitats preferences.
Key-words: ecomorphology, fish, floodplain lakes, Amazon.

RESUMO: Similaridades ecomorfológicas de treze espécies de peixes dominantes de lagos de várzea da Amazônia. Atributos ecomorfológicos de treze espécies de peixes de lagos de várzea da Amazônia foram estimados e relacionados com o hábito alimentar. Uma forte relação entre a morfologia e os hábitos alimentares, foi obtida mas a morfologia também pode ser um importante indicador de preferências pelo uso de habitats.
Palavras-chave: ecomorfologia, peixe, lagos de várzea, Amazônia.

Introduction

The influence of biotic and abiotic factors as structuring forces of natural communities has a long history of controversy in ecological literature (Jackson, 1994). Roughgarden (1983) suggested the best way to analyze it is inferring the competitive coevolution through building and presenting convincing cases based on various sources of circunstantial evidence that include evidence of the competition from descriptive and experimental data, morphological patterns, and species lists.

The ecomorphology aim to identify how the organisms are built and the evolutionary consequences to final design, diminishing the subjectivity by the quantitative approach. The main idea is that the morphological differences between species can be associated with environmental conditions (Beaumord & Petrere Jr., 1994). These differences can be evaluated by the use of morphometrics and biometrics indices (Wikramanayake, 1990). Usually, these indices are interpreted as indicators of life strategies or adaptations to successful colonization of habitats (Beaumord & Petrere Jr., 1994; Motta et al., 1995).

Most natural aquatic environments support characteristic fish assemblages, which have developed over evolutionary time (Araújo & Santos, 2001). Floodplain environments are dynamic systems that exhibit high productivity and support important inland fishing activities. These systems are markedly influenced by the hydrological cycle with distinct aquatic-terrestrial phases that influence the community's composition. The fish that inhabit floodplain lakes developed several morphological and physiological adaptations to successful explore these complex systems and its seasonal changes (Junk et al., 1997; Saint-Paul et al., 2000).

Floodplain Amazonian fish exhibit high morphological and ecological diversity (Goulding, 1980; Pouilly et al., 2003). They occupy a wide variety of ecological niches, forage on almost everything of energetic value, and demonstrate a full range of life

habitats and feeding styles (Ferreira, 1981; Soares et al., 1986; Merona et al., 2001). In this paper we focus on various ecomorphological attributes to describe some predominant fish species of floodplain lakes and relate then to the feeding habits aiming contribute to identify patterns of resource use.

Material and methods

Study area

The fish were collected in five floodplain lakes located on the lower stretch of Solimões River (Fig. 1), nominally: Preto Lake (S 03° 20' 39"/W 060° 35' 22"), Iauara Lake (S 03° 36' 20"; W 061° 18' 16"), Campina Lake (S 03° 46' 14"; W 062° 22' 01"), Poraqué lake (S 03° 57' 81"; W 063° 09' 93"), and Aruã Lake (S 04° 06' 29"; W 063° 32' 10").

All these lakes are subject to four seasons markedly distinct, determined by the hydrological cycle. During the dry season, the lakes are not connected to the river. They are shallow and generally hypoxic. During the flood season, these lakes are connected to the river and the nutrient inputs are high. The other two seasons are characterized by the moving waters, rising and receding, and they have a major influence on the productivity of whole system.
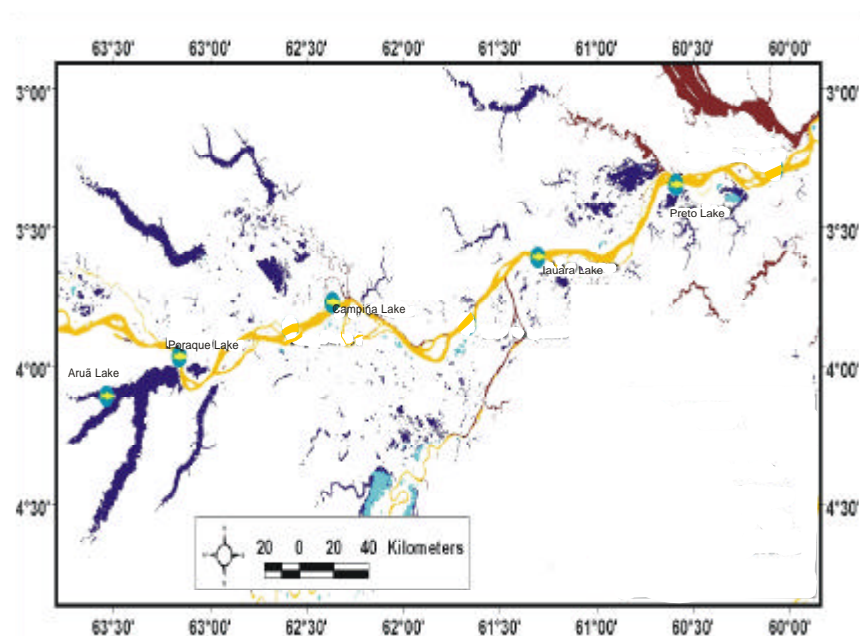

Figure 1: Study area indicating of sampling sites.

Sampling Program

Four samplings were performed from January 2003 to November 2003, with intervals of approximately three months. The samplings were taken with gillnets. The nets had standardized dimensions of 30 m long and 2.5 m height, with mesh size of 30, 40, 50, 70 and 90 mm between adjacent knots. In the samplings, the gillnets were set up close to the lake edge at sunrise and removed at sunset of the same day, remaining for 12 hours in the water. Immediately before the catch, the fish were kept in a 10% formaline solution. At the Fishing Ecology Laboratory at the Federal University of Amazonas the fish were washed, measured, weighed and preserved in a 70% alcohol solution. The fish were identified following Gery (1977), Kullander (1986) and by experts.

Morphometric Measurements and Data Analysis

Morphometrics measurements were performed on 109 fish belongs to thirteen fish species with the most abundance and frequency during the experimental fisheries (Tab. I and III). It belongs to Characiformes and Perciformes orders that were dominant in the Amazonian floodplain lakes. We use only adult fish aiming to avoid alometric effects.

Table I: Species list with code, scientific name, sampling size and main diet. AP = algae and periphyton, AM = aquatic macrophytes, INV = invertebrates aquatic and terrestrial, MUD = soft substratum, PM = planktonic micro crustaceans, BM = benthonic micro crustaceans, SE = seeds, MP = material plant, FI = fins, S = scales, F = flesh fish.

Code	Species / Family	N	Trophic level	Main food	References
AC	Acarichthys heckellii (Müller & Troschel, 1849) Cichlidae	6	Omnivore	MP, INV, MUD	Knoppel, 1970; Ferreira, 1993; Reis & Caramaschi, 1999; Claro Jr., 2003
CM	Colossoma macropomum (Cuvier, 1818) Serrasalmidae	6	Omnivore	SE, PM, INV	Goulding, 1980; Goulding & Carvalho, 1982; Silva et al., 2000
GE	Geophagus spp. / Cichlidae	9	Invertivore	INV	Ferreira, 1993
CF	Chaetobranchus flavescens (Heckel, 1840) Cichlidae	10	Zooplanktivore	PM	Lowe McConnell, 1969; Ribeiro, 2002
PY	Pygocentrus nattereri (Kner, 1860) Serrasalmidae	8	Piscivore	F, INV	Merona et al., 2001; Pouilly et al., 2003; Piorski et al., 2005
SA	Satanoperca acuticeps (Heckel, 1840) Cichlidae	9	Omnivore	INV, BM, S	Ferreira, 1993; Reis & Caramaschi, 1999
SE	Serrasalmus elongatus (Kner, 1858) Serrasalmidae	10	Piscivore	F, S, FI	Ferreira, 1993; Claro Jr., 2003
MH	Metynnis hypsauchen (Muller & Troschel, 1844) Serrasalmidae	10	Herbivore	AM, AP, SE	Ferreira, 1993; Claro Jr., 2003
SG	Serrasalmus eigenmanni (Norman, 1929) Serrasalmidae	8	Piscivore	F, FI, INV, PM	Ferreira, 1993; Merona et al., 2001; Claro Jr., 2003; Pouilly et al., 2003
SC	Serrasalmus calmoni (Steindachner, 1908) Serrasalmidae	6	Piscivore	F	Merona et. al., 2001
SS	Serrasalmus spilopleura (Kner, 1858) Serrasalmidae	7	Piscivore	F, FI, INV, PM	Ferreira, 1993; Merona et al., 2001; Claro Jr., 2003
HR	Heros severus (Heckel, 1840) Cichlidae	10	Herbivore	AP, MP	Ferreira, 1981; Soares et al., 1986; Ferreira, 1993; Merona et al., 2001
UA	Uaru amphiacanthoides (Heckel, 1840) Cichlidae	10	Herbivore	AP, MP, MUD	Ferreira, 1993; Reis & Caramaschi, 1999.

The morfometrics measures were made according to the criteria proposed by Gery (1977) and Kullander (1986). The body and fins area were estimated by measures of its outline according to Beaumord (1991). For all species, we made the following

measures: (1) standard length, (2) caudal peduncle width, (3) caudal peduncle height, (4) caudal peduncle length, (5) maximum body width, (6) body height maximum, (7) head length, (8) width mouth, (9) depth media line eye; (10) height media line body; (11) pectoral fin width maximum; (12) pectoral fin length maximum; (13) posterior caudal fin height; (14) anterior caudal fin height; (15) caudal fin area; (16) maximum head height; (17) pectoral fin area; (18) caudal fin extension maximum (Smith, 1999; Wikramanayake, 1990; Beaumord & Petrere Jr, 1994; Matheus-Chan, 2001; Gatz, 1979). The main diet for each species was identified from literature (Tab. I).

Based on morphometric measurements we estimated seven ecomorphological attributes described in the Table II. A cluster analysis was accomplished aiming to identify species groups using ecomorphological attributes as descriptors. We used the minimum variance method as amalgamation rule and the Chebychev metric estimate as distance measure (Ludwig & Reynolds, 1988). A correspondence analysis was performed aiming to corroborate the clusters and to identify which ecomorphological attributes was the most relevant for ordination (McGarigal, 2000).

Table II: Ecomorphological attributes its estimation and interpretation.

Ecomorphological attributes	Code	Estimation	Interpretation
Compression index	CI	Maximum body depth divided by maximum body width	High values indicate a laterally compressed fish, and would be expected in fish occupying habitats with low water velocity (Watson and Balon, 1984).
Relative depth	RD	Maximum body depth divided by standard length	Assumed to be inversely related to habitat water velocity and directly related for capacity to making vertical turns (Gatz, 1979).
Caudal peduncle compression index	CPC	Caudal peduncle depth divided by caudal peduncle width	A compressed peduncle would indicate the habit of slow swimming and maneuver ability (Gatz, 1979)
Flattening ventral index	IVI	Proportion of body depth below the midline at the point of maximum depth	Low index would be associated with life in fast flowing water by assisting the fish to maintain a position without swimming (Gatz, 1979).
Pectoral aspect fin	FAP	Maximum length of fin divided by maximum width	A high ratio indicates a long, narrow pectoral fin which it is expected among fish which swing a great deal (Keast & Webb, 1966)
Relative area of caudal fin	RFC	Area of caudal fin divided by the area of the body	Large caudal fins are important for fast start burst the typical swimming mode of most benthic fish (Balon et. al., 1986)
Relative eye position	RPE	Proportion of head depth which occurs below the middle or the eye	Benthic fish has more dorsally located eyes, whereas those of nektonic fish tends to be more lateral (Gatz, 1979)

Results

First, the cluster analysis isolated a small and homogeneous group made up of two cichlids, Heros severus and Uaru amphiacanthoides (Fig 2). These two cichlids are herbivore and feed mainly on algae and periphyton associated with soft substratum (Tab. I). A further separation shaped two more heterogeneous groups having defined another two heterogeneous groups. The first is predominantly formed by piscivorous Serrasalmus calmoni, Serrasalmus eigenmanni, and Serrasalmus spilopleura, and by herbivore Metynnis hypsauchen. The second group is very heterogeneous and it

was composed by omnivore, herbivore and planktivore species. However, a new division of this group will result in more homogeneous groups. The first is composed by Acarichthys heckellii, Colossoma macropomum, Geophagus sp., and Chaetobranchus flavescens; and, the second by Pygocentrus nattereri, Satanoperca acuticeps, and Serrasalmus elongatus (Fig. 2).

The correspondence analysis extracted the two first dimensions which explain more than 95% of total variance (Fig. 3). Dimension 1 explains 71.65%, and dimension 2 explains 24.12%. The first dimension is stronger and it distinguished the cichlids H. severus and U. amphiacanthoides of all species due to high values of caudal peduncle compression index (CPC) (Tab. III). The second dimension discriminate a group composed by P. nattereri, S. acuticeps, and S. elongatus due to the estimates of the relative area of caudal fin (RFC), relative eye position (RPE) and pectoral aspect fin (FAP). Another group is composed by two species of piranha S. spilopleura and S. calmoni and M. hypsauchen that was associated with relative
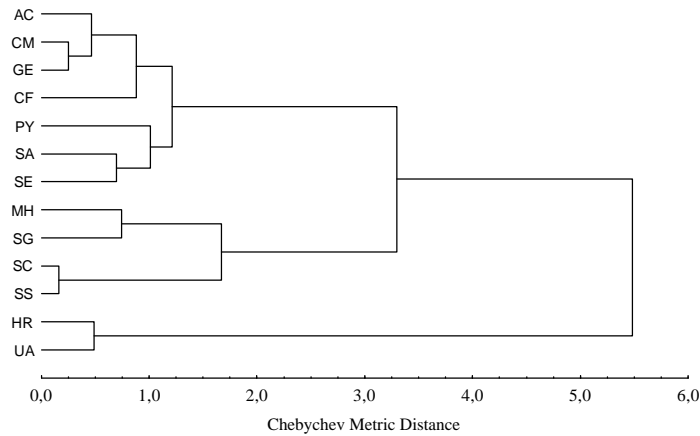

Figure 2: Cluster analysis dendograma for fish species second its ecomorphological attributes (species codes see Table I).
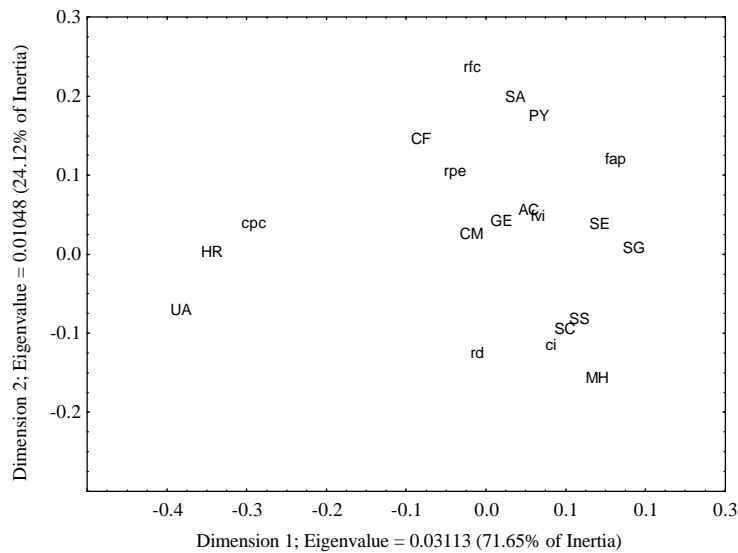

Figure 3: First two dimensions of correspondence analysis (species and attributes codes see Table I).

depth (RD) and compression index (CI) (Fig. 3). C. macropomum, A. heckelii, and Geophagus sp. showed a median position indicating intermediary values for the attributes IVI, RPE, FAP, RD and CI (Fig. 3; Tab.III). We use the information on the feeding habits, acquired from several works previously accomplished (Tab. I).

Table III: Mean values of the ecomorphological attributes to each species (codes see Tab.I and Tab.III)

	Ci	Rd	cpc	Fvi	rfc	Fap	Rpe
AC	2.942	0.454	2.389	0.399	3.240	0.158	0.747
CF	2.295	0.414	2.786	0.453	3.124	0.181	0.614
CM	3.178	0.533	1.830	0.511	2.894	0.130	0.508
GE	2.727	0.432	2.391	0.313	2.901	0.136	0.726
PN	2.864	0.544	2.054	0.475	2.468	0.112	0.559
AS	2.417	0.393	2.554	0.360	3.791	0.165	0.691
SE	3.023	0.391	1.831	0.500	3.022	0.119	0.516
MH	4.641	0.775	2.221	0.519	3.500	0.114	0.547
SG	3.892	0.537	2.095	0.535	4.123	0.105	0.586
SC	3.908	1.220	2.048	0.492	3.067	0.216	0.526
SS	3.511	0.567	1.977	0.492	2.959	0.104	0.543
HR	2.782	0.571	4.219	0.410	2.173	0.135	0.630
UA	3.269	0.591	4.755	0.451	1.910	0.107	0.680

Discussion

The thirteen fish species encompass a relatively homogeneous group that have a compressed and discoid body shape, typical of Serrasalmidae and Cichlidae. The Cichlidae are more diversified in shape than Serrasalmidae, probably due to the greater diversity of life strategies (Kullander, 1986). The Cichlidae is a group with more than 1000 species, distributed in South America and Africa. The major number of South American species is in the Amazon basin and have several adaptations connected to feeding (Lowe McConnell, 1969; Kullander, 1986). Pygocentrus nattereri, Serrasalmus elongates, S. eigenmanni, S. calmoni, S. spilopluera and Metynnis hypsauchen are Serrasalmidae, which is a group with 15 endemic genera and 80 species from Neotropical Region (Gery, 1977). In the Amazon basin, these fish feed on fish, fruits and invertebrates (Goulding, 1980 ; Reis et al., 2003). This broad use of feeding resources can be an indicator of the existence of an unspecified organizing principle driving fish assemblage structure (Douglas & Matthews, 1992).

The caudal peduncle compression index (CPC) is determinant for clustering of H. severus and U. amphiacanthoides. In general, high values for this index are linked to slow swim and low maneuverability and reduce the ability for fast departures (Gatz, 1979), specially in species with long body. The values of CPC can be explained by the diets of these species that is composed predominantly by leaves, algae and micro-algae found at submersed debris, placed at shallow areas of lakes (Ferreira, 1981; Reis & Caramaschi, 1999).

High values of compression index (CI) and relative depth (RD) represents easiness for vertical shunting (Gatz, 1979; Watson & Balon, 1984), while the low values of relative caudal fin area indicate slow swim typical of lentic fish species (Balon et al., 1986). Several species of piranhas (Serrasalmus and Pygocentrus) and pacus (Mylossoma) are associated with macrophytes banks (Sanchez-Botero & Araújo-Lima (2001; Petry et al., 2003). We believe that the correlation of M. hypsauchen, S. spilopleura and S. calmoni with these compression index (CI) and relative depth (RD) attributes can be explained by the use of macrophytes banks for feeding,

reproduction and/or refuge banks (Henderson & Hamilton, 1995; Sanchez-Botero & Araújo-Lima, 2001; Petry et al., 2003). Probably, the high complexity of these habitats takes advantage for the coexistence of species of different trophic levels (Araújo-Lima et al., 1986; Petry et al., 2003) and maybe different morphologic characteristics.

High values of relative area of caudal fin (RFC), relative eye position (RPE) and pectoral aspect fin (FAP) are typical attributes of fish that swim a great deal (Keast & Webb, 1966), and are able to fast start burst (Balon et. al., 1986). P. nattereri, S. acuticeps, and S. elongatus are species with great adaptative ability to explore several habitats in the floodplain lakes. The swiming skill allows the piranhas to explore the water column (Nico & Taphorn, 1988; Petry et al., 2003) and the cichlid the bottom for feeding (Reis & Caramaschi, 1999).

The more generalist characteristics of ecomorphological attributes for C. macropomum, C. flavescens, Geophagus sp. and A. heckelii are probably result of the influence of several kinds of feeding that include fitoplankton, zooplankton, fruits, microcrustaceans and insects (Knoppel, 1970; Soares et al., 1986; Ferreira, 1993; Ribeiro, 2002; Claro Jr., 2003). A. heckelii, Geophagus sp. are predominantly benthopelagics (Knoppel, 1970; Ferreira, 1993; Reis & Caramaschi, 1999; Claro Jr., 2003). C. macropomum and C. flavescens are midwater feeder (Lowe McConnell, 1969; Goulding, 1980; Reis & Caramaschi, 1999). The feeding of C. macropomum and C. flavescens is mainly composed by planktonic microcrustaceans (Goulding & Carvalho, 1982; Lowe McConnell, 1969). Besides C. macropomum also eat fruits found in the flooded forest during the flood season (Goulding & Carvalho, 1982). The morphology of these species directly reflects their ability to use various food sources and habitats in Amazonian floodplain lakes (Pouilly et al., 2003; Reis & Caramaschi, 1999). Nevertheless, two species can explore different food resources and have the same body shape as it was observed to M. hypsauchen (herbivore) and S. spilopleura (piscivore) that inhabit aquatic macrophytes.

Douglas & Matthews (1992) argued that adaptations by North American stream fish appear most possible within distinct morphological constraints imposed by phylogeny at the family level. We agreed that competition may be important in structuring freshwater fish assemblages, but predominantly within genera and particularly between recently evolved forms. Finally, we believe that morphological adaptations and trophic diversity can be very important to permit the coexistence of species in the Amazonian fish assemblages. Nevertheless, other studies with appropriate tests would be employed to evaluate this important ecological question.

Acknowledgements

References

Araújo-Lima, C.A.R.M., Portugal, L.P.S. & Ferreira, E.J.G. 1986. Fish-macrophyte relationship in Anavilhanas Archipelago, a black water system in the Central Amazon. J. Fish Biol., 29:1-11.

Araújo, F.G. & Santos, L.N. 2001. Distribution of fish assemblages in Lajes Reservoir, Rio de Janeiro, Brazil. Braz. J. Biol., 61:563-576.

Balon, E.K., Crawford, S.S. & Lelek, A. 1986. Fish communities of the upper Danube river (Germany, Austria) prior to the new Rheinmain-Donau connection. Environ. Biol. Fishes, 15:243-271.

Beaumord, A.C. 1991. As comunidades de peixes do rio Manso, Chapada dos Guimarães-MT: uma abordagem ecológica numérica. Rio de Janeiro, UFRJ, 107p (Dissertação).

Beaumord, A.C. & Petrere Júnior, M. 1994. Fish communities of Manso river, Chapada dos Guimarães, MT, Brazil. Acta Biol. Venez., 15:21-35.

Claro Jr., L.H. 2003. A influência da floresta alagada na estrutura trófica de comunidades de peixes em lagos de várzea da Amazônia Central. INPA-UFAM, Manaus. 61p (Master Thesis).

Douglas, M.E. & Matthews, W.J. 1992. Does morphology predict ecology? Hypothesis testing within a freshwater stream fish assemblage. Oikos, 65:213-224.

Ferreira, E.J.G. 1981. Alimentação de adultos de doze espécies de peixes cichlídeos (Perciformes, Cichlidae) do rio Negro, Brasil. INPA-UFAM, Manaus. 242p. (Master Thesis).

Ferreira, E.J.G. 1993. Composição, distribuição e aspectos ecológicos da ictiofauna de um trecho do rio trombetas, na área de influência da futura UHE Cachoeira Porteira, estado do Pará, Brasil. Acta Amazonica, 23 (supl.):1-89.

Gatz Jr., A.J. 1979. Community organization in fishes as indicate by morphological features. Ecology, 60:711-718.

Gery, J. 1977. Characoids of the world. TFH Publications. Neptune City, New Jersey. 672p.

Goulding, M. 1980. The fishes and the forest. Explorations in Amazonian natural history. University of California Press, Berkeley. 280p.

Goulding, M. & Carvalho, M.L. 1982. Life history and management of tambaqui (Colossoma macropomum, Characidae), an important Amazonian food fish. Rev. Brás. Biol., 1:107-133.

Henderson, P.A. & Hamilton, H.F. 1995. Standing crop and distribution of fish in drifting and attached floating meadow within and Upper Amazonian varzea lake. J. Fish Biol., 47:266-276.

Jackson, J.B.C. 1994. Community unity? Science, 264:1412-1413.

Junk, W.J., Soares, M.G.M. & Saint-Paul, U. 1997. The fish. In: Junk, W.J. (ed.) The Central-Amazonian floodplain: ecology of a pulsing system. Springer Verlag, Berlin, p.385-408. (Ecological studies, v.126)

Keast, A. & Webb, D. 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake Opinicon, Ontario. J. Fish. Res. Board. Can., 23:1845-1874.

Knoppel, H. 1970. Food of central Amazonian fishes contribution to the nutrient-ecology of Amazonian rain-forest-streams. Amazoniana, 2:237-352.

Kullander, S.O. 1986. Cichlid fishes of the Amazon River drainage of Peru. Swedish Museum of Natural History, Stockholm. 431p.

Lowe McConnell, R.H. 1969. The Cichlid fishes of Guyana, South America, with notes on their ecology and breeding behavior. Zoological. J. Linn. Soc., 48:255-302.

Ludwig, J.A. & Reynolds, J.F. 1988. Statistical ecology. A primer on methods and computing. John Wiley & Sons Inc., New Yok. 337p.

Mathews-Chan, D. 2001. Fish ecomorphology: predicting habitat preferences of streams fishes from their body shape. Virginia, Faculty Virginia Polytechnic Institute and State University, p.269 (Dissertation).

McGarigal, K., Cushman, S. & Stafford, S. 2000. Multivariate statistics for wildlife and ecology research. Springer-Verlag, New York. 283p.

Merona, B., Santos, G.M. & Almeida, R.G. 2001. Short terms effects of Tucuruí Dam (Amazônia, Brazil) on the trophic organization of fish communities. Environ. Biol. Fishes, 60:375-392.

Motta, P.J., Clifton, K.B., Hernandez, P. & Eggold, B.T. 1995. Ecomorphological correlates in ten species of subtropical seagrass fishes: diet and microhabitat utilization. Environ. Biol. Fishes, 44:36-60.

Nico, L.G. & Taphorn, D.C. 1988. Food habits of piranhas in the low llanos of Venezuela. Biotropica, 20:311-321.

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

Piorski, N.M., Alves, J.R.L., Machado, M.R.B. & Correia, M.M.F. 2005. Alimentação e ecomorfologia de duas espécies de piranhas (Characiformes: Characidae) do lago de Viana, Estado do Maranhão, Brasil. Acta Amazônica, 35:63-70.

Pouilly, M., Lino, F., Bretenoux, J.G. & Rosales, C. 2003. Dietary-morphological relationships in a fish assemblage of the Bolivian Amazonian floodplain. J. Fish Biol., 62:1137-1158.

Reis, R.A. & Caramaschi, E.P. 1999. Feeding habits of nine cichlideos found in Batata Lake (Porto Trombetas, PA, Brazil). In: Val, A.L. & Almeida-Val, V.M.F (eds.) Biology of tropical fishes. Manaus. p.127-136.

Reis, R.E., Kullander, S.O. & Ferraris, C.J. 2003. (eds.) Check list of freshwater fishes of South and Central América. Edipucrs, Porto Alegre. 729p.

Ribeiro, A. de L. 2002. Alimentação, morfologia e morfometria do aparelho digestório de Chaetobranchus flavescens (Heckel, 1840) do lago Camaleão. Manaus, Universidade Federal do Amazonas, 30p (Monografia).

Roughgarden, J. 1983. Competition and theory in community ecology. Am. Nat., 122:583-601.

Saint-Paul, U., Zuanon, J., Villacorta-Correa, M.A., Garcia, M., Fabré, N.N., Berger, U. & Junk, W.J. 2000. Fish communities in Central Amazonia white and black waters floodplains. Environ. Biol. Fishes, 57:235-250.

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

Silva, J.A.M., Pereira-Filho, M. & Oliveira-Pereira, M.I. 2000. Seasonal variation of nutrients and energy in tambaqui (Colossoma macropomum Cuvier, 1818) natural food. Rev. Bras. Biol., 60:599-605.

Smith, W.S. 1999. A ecomorfologia de peixes no Brasil. Bol. Soc. Bras. Ictiol., 56:8-12.

Soares, M.G.M., Almeida, R.G. & Junk, W.J. 1986. The tropic status of the fish fauna in lago Camaleão e macrophyte dominated floodplain lake in the middle Amazon. Amazoniana, 9:511-526.

Watson, D.J. & Balon, E.K. 1984. Ecomorphological analysis of fish Taxocenes in rainforest streams of northern Borneo. J. Fish Biol., 25:371-384.

Wikramanayake, E.D. 1990. Ecomorphology and biogeography of a tropical stream fish assemblage: evolution of assemblage structure. Ecology, 71:1756-1764.