Feeding ecology of *Pterodoras granulosus* (Siluriformes, Doradidae) in the Lajeado Reservoir, Tocantins, Brazil

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ABSTRACT. The diet and feeding habits of armado catfish, *Pterodoras granulosus* (Valenciennes, 1821), were studied in the Lajeado Reservoir, Tocantins, Brazil, and the mouth of its tributaries. Stomach contents of 327 specimens were analyzed by the percentage composition and volumetric methods. The feeding of armado on a wide variety of foods, including both animal and plant items, leads to its classification as a euriphagic species with herbivorous tendency. However, it should be noted that armado showed a strong ontogenetic diet shift, with the gradual replacement of detritus and sediment by plant items, especially terrestrial ones. The environmental use pattern of *P. granulosus* corroborates the ontogenetic shift observed in its diet. Small fish predominated mainly in the benthic region and detritus and sediment represented an important resource, whereas large fish fed mainly on terrestrial plants, as they explore open water sites and the surface of the water column.

KEYWORDS. Feeding habits, seasonal shift, ontogenetic shift, habitat use.

RESUMO. Ecologia alimentar de *Pterodoras granulosus* (Siluriformes, Doradidae) no reservatório do Lajeado, Tocantins, Brasil. Foi investigada a dieta e o hábito alimentar do armado, *Pterodoras granulosus* (Valenciennes, 1821) no reservatório do Lajeado, Tocantins e na foz de seus tributários. Conteúdos estomacais de 327 exemplares foram analisados através dos métodos de composição percentual e volumétrico. A utilização de uma ampla variedade de tipos de itens alimentares pelo armado, incluindo itens de origem animal e vegetal permite classificar esta espécie como eurifágica, com tendência à herbivoria. No entanto, deve ser considerado que esta espécie apresenta uma forte variação ontogenética na dieta. Foi constatada uma redução gradual na participação de detrito e sedimento na dieta em detrimento dos itens de origem vegetal, especialmente os terrestres. O padrão de utilização do ambiente por *P. granulosus* está de acordo com a variação ontogenética observada na dieta do armado. Enquanto os indivíduos pequenos utilizam predominantemente a região bentônica e têm o detrito e sedimento como itens importantes na composição da dieta os indivíduos de maior porte utilizam áreas abertas e superficiais da coluna da água tendo os vegetais terrestres como principal item da dieta.

PALAVRAS-CHAVE. Hábito alimentar, variação sazonal, variação ontogenética, uso do habitat.

The armado catfish, *Pterodoras granulosus* (Valenciennes, 1821), is a migrating endemic siluriform of the Amazon and La Plata basins (Ringuelet *et al*., 1967; Bonetto *et al*., 1971; Agostinho *et al*., 1994, 2003; Makrakis *et al*., 2007). Females reach sexual maturity at six years of age (Feitoza *et al*., 2004), measuring approximately 36 cm in length (Agostinho *et al*., 1994). This is the main species caught by commercial fishers in the Itaipu Reservoir on the Paraná River (Agostinho *et al*., 2003). In addition to its importance for fishing, it has been pointed out as being ecologically significant in the population control and/or dispersal of animals and plants (Slootweg *et al*., 1993; Stevaux *et al*., 1994; Darrigran & Colautti, 1994; Pilati *et al*., 1999; Ferriz *et al*., 2000; Cantanhêde *et al*., 2008). Studies on the feeding habits of the armado catfish acknowledge its omnivorous nature (Hahn *et al*., 1992, 1997; Gaspar da Luz *et al*., 2002), despite its main herbivorous tendency (Hahn *et al*., 1992). In addition to plants, aquatic insect larvae and molluscs are important resources for this fish (Ringuelet *et al*., 1967; Hahn *et al*., 1992).

Although *P. granulosus* is not abundant in fluvial environments of the Tocantins River basin, this species has been commonly captured in experimental fisheries carried out in reservoirs (Carlos S. Agostinho, pers. obs.). Its high potential to colonize reservoirs may be related to its great feeding plasticity, since this species tend to consume the most abundant food resources in the environment (Panattieri & Del Barco, 1981; Ferriz *et al*., 2000).

Despite the complex trophic relations of tropical freshwater ecosystems, feeding studies can contribute to the understanding of the ecological role of the species and how they respond to environmental changes resulting from damming. We analyzed the diet of *P. granulosus* in the Lajeado Reservoir in order to clarify the following questions: the feeding habits of the armado catfish; seasonal and/or ontogenetic dietary shifts; environmental use patterns associated with individual size and the species feeding habits related to its pattern of environmental.

MATERIAL AND METHODS

The Lajeado Reservoir, completed in February 2002, is located on the Tocantins River between 11°49'S, 48°38'W, and 09°45'S, 48°21'W. It covers 626 km^2 and is approximately 172 km long and 8.8 m deep on average, reaching 40 m deep near the dam. Mean water residence time is 24 days, and the average surface water velocity is 0.083 m/s. Specimens were collected at 10 locations: seven in the main body of the reservoir and three in the confluence of tributaries (Fig. 1).

Sampling was carried out monthly from April 2002 to August 2004, using gill nets (20 m long and 2 m high) with mesh sizes ranging from 2.4 to 18.0 cm. The gill nets were set parallel to the shores at epipelagic, littoral, and bathypelagic (around 20 m deep) environments of the reservoir. Nets remained deployed for 24 h/month at every sampling site. Individuals caught were measured and had their stomachs removed and preserved in 4% formalin.

Stomach contents were identified and the volume was measured through displacement of water in a graduate cylinder. The volume of small items was estimated as a percentage of the total food item volume. Specie diet was evaluated using percentage composition and volumetric methods (HYSLOP, 1980). Percentage composition was defined as a percentage of occurrences of each food item in relation to the occurrence of all food items.

Diet composition, food item origin (aquatic, terrestrial, or undetermined), and diet breadth were analyzed for different standard length classes. These classes were defined arbitrarily in 5.5 cm intervals, in order to distribute a reasonable number of stomachs per class and adequately evaluate the diet in the full range of fish size. Diet breadth was calculated based on item volumes using the Levins index (Levins, 1968 *apud* KREBS, 1989). Hurlbert (1978) *apud* KREBS (1989) proposed that values close to zero indicate specialist habit, while values close to one indicate generalist habit.

The diet composition (volume data) of small and large individuals in the dry (July to September) and rainy (December to February) seasons were compared using Spearman Correlation Tests (r_s).

The pattern of environmental use was analyzed by length classes based on the percentage of individuals caught in the epipelagic, littoral, and bathypelagic zones.

RESULTS

Analyses showed that *P. granulosus* consumed a wide range of food items, including both aquatic and terrestrial items, from animal and plant sources. Among animal items, the majority were invertebrates, especially larvae and pupae of chironomidae (6.83 of percentage composition and 0.62% of volume), ostracoda (6.47 and 0.25%) and bivalves (1.71 and 3.95%). Plant items that most contributed to the fish diet were terrestrial (12.63 and 41.43%) and aquatic (7.14 and 18.41%), fruit and seeds (6.83 and 13.07%), and filamentous algae (4.94 and 2.00%). Detritus and sediment were also important components of the diet (19.95 and 10.46%) (Tab. I).

The main diet components (volume values) (insects, plants, and detritus/sediment) showed a reduction in detritus and an increase in plants as the fish grows, especially above 22.5 cm (Fig. 2). Terrestrial items were also more important above this length (percentage composition) (Fig. 3) and the diet breadth was reduced, indicating that large individuals have a more specialized diet (Fig. 4). This result is not applicable to very small individuals (6-11.5 cm), as the number of stomachs analyzed was too small.

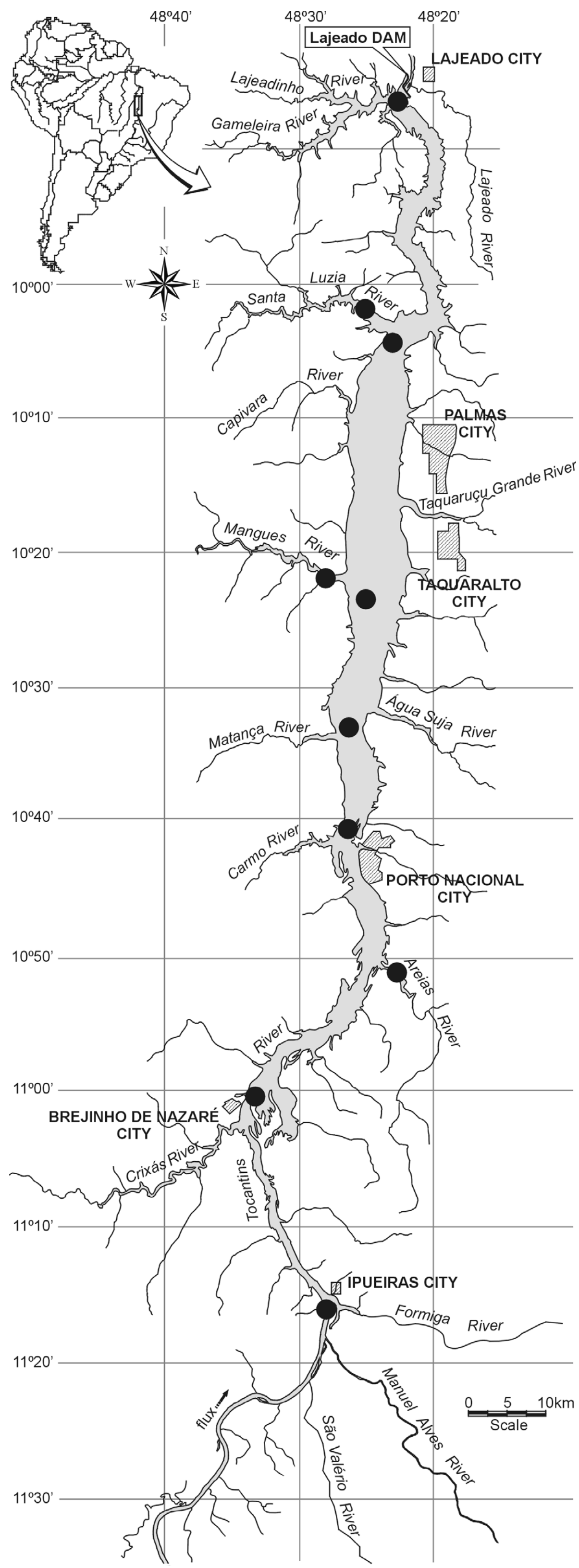
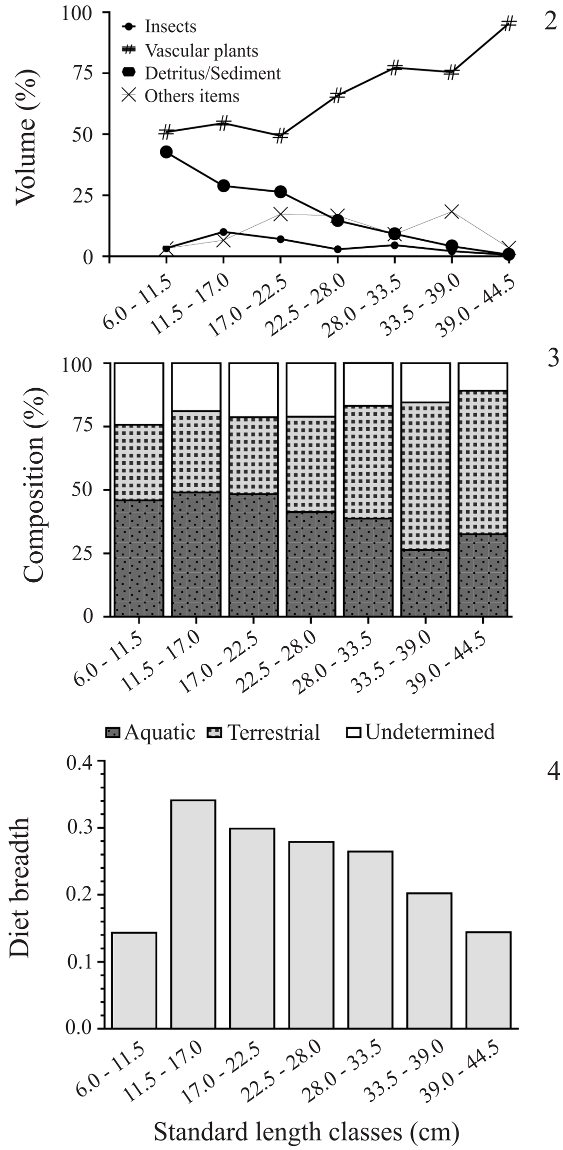


Figure 1. Location of the study area and sampling sites in the Lajeado Reservoir, Tocantins, Brazil.

Table I. Food items origin, percentage composition (PCO%) and volume frequency (VOL%) by fish standard length average (Ls) as a function of stomach contents of *Pterodoras granulosus* (Valenciennes, 1821), in the Lajeado Reservoir, Tocantins, Brazil, April 2002 to August 2004 (n, number of analyzed stomachs).

ITEMS	ORIGIN	Ls = 6.0 to 22.5 cm n = 201		Ls = 22.5 to 60.2 cm n = 126		TOTAL n = 327	
		PCO (%)	VOL (%)	PCO (%)	VO L (%)	PCO (%)	VOL (%)
INSECT - TERRESTRIAL STAGES		15.42	6.56	13.71	1.64	14.83	2.67
Coleoptera	Terrestrial	1.31	0.23	0.88	0.07	1.16	0.11
Diptera	Terrestrial			0.18	0.00	0.06	0.00
Ephemeroptera	Terrestrial	2.71	0.26	1.41	0.08	2.26	0.11
Hemiptera	Terrestrial	0.37	0.01			0.24	0.00
Hymenoptera	Terrestrial	1.40	0.08	1.23	0.33	1.34	0.28
Isoptera	Terrestrial			0.18	0.04	0.06	0.03
Odonata	Terrestrial	0.19	0.04	0.53	0.09	0.31	0.08
Orthoptera	Terrestrial			0.18	0.01	0.06	0.01
Trichoptera	Terrestrial	0.19	0.00	0.18	0.00	0.18	0.00
Insect remains	Terrestrial	9.25	5.95	8.96	1.01	9.15	2.04
INSECT - AQUATIC STAGES		11.21	1.41	8.79	0.83	10.37	0.95
Ephemeroptera larva and nymph	Aquatic			0.18	0.01	0.06	0.01
Ceratopogonidae larva and pupa	Aquatic	1.59	0.08	0.88	0.09	1.34	0.09
Chaoboridae larva and pupa	Aquatic	0.75	0.06	0.18	0.06	0.55	0.06
Chironomidae larva and pupa	Aquatic	7.76	1.17	5.10	0.47	6.83	0.62
Culicidae larva and pupa	Aquatic			0.53	0.04	0.18	0.04
Hymenoptera larva and pupa	Aquatic			0.35	0.03	0.12	0.02
Lepidoptera larva and pupa	Aquatic			0.88	0.11	0.31	0.08
Plecoptera larva and pupa	Aquatic			0.18	0.00	0.06	0.00
Trichoptera larva and pupa	Aquatic	1.12	0.10	0.53	0.01	0.92	0.03
MICROCRUSTACEANS		13.93	1.08	3.51	0.20	10.31	0.38
Cladocera	Aquatic	4.21	0.25	0.35	0.05	2.87	0.10
Copepoda	Aquatic	0.47	0.01			0.31	0.00
Ostracoda	Aquatic	8.22	0.66	3.16	0.14	6.47	0.25
Microcrustaceans remain	Aquatic	1.03	0.16			0.67	0.03
OTHER INVERTEBRATES		1.68	0.19	2.99	3.18	2.14	2.56
Arachnida	Terrestrial	1.50	0.16	0.70	0.01	1.22	0.05
Diplopoda	Terrestrial			0.88	0.53	0.31	0.42
Chilopoda	Terrestrial			0.18	0.00	0.06	0.00
Oligochaeta	Aquatic	0.19	0.02	0.53	2.38	0.31	1.88
Decapoda	Aquatic			0.70	0.25	0.24	0.20
MOLLUSC		2.43	2.32	5.27	6.30	3.42	5.47
Bivalvia	Aquatic	1.03	1.51	2.99	4.60	1.71	3.95
Gastropoda	Aquatic	1.21	0.80	2.28	1.70	1.59	1.51
Molluscs remains	Aquatic	0.19	0.01			0.12	0.00
PROTOZOA		1.31	0.04	0.35	0.04	0.98	0.04
Tecameba	Aquatic	1.31	0.04	0.35	0.04	0.98	0.04
FISH		3.55	0.95	3.51	1.54	3.54	1.41
Fish	Aquatic	3.55	0.95	3.51	1.54	3.54	1.41
VASCULAR PLANTS		23.83	50.91	35.15	79.56	27.76	73.56
Aquatic	Aquatic	6.73	16.24	7.91	18.99	7.14	18.41
Terrestrial	Terrestrial	10.75	19.12	16.17	47.34	12.63	41.43
Fruit/seeds	Terrestrial	5.05	13.91	10.19	12.85	6.83	13.07
Briophyta	Aquatic	1.31	1.63	0.88	0.38	1.16	0.64
ALGAE		7.85	9.37	3.87	0.16	6.47	2.08
Filamentous algae	Aquatic	5.98	8.99	2.99	0.15	4.94	2.00
Non filamentous algae	Aquatic	1.87	0.38	0.88	0.01	1.53	0.08
FUNGI				0.70	0.54	0.24	0.42
Fungi	Aquatic			0.70	0.54	0.24	0.42
DETRITUS/SEDIMENT		18.79	27.19	22.14	6.03	19.95	10.46
Detritus/sediment	Undetermined	18.79	27.19	22.14	6.03	19.95	10.46



Figures 2-4. Stomach contents of *Pterodoras granulosus* (Valenciennes, 1821), in the Lajeado Reservoir, Tocantins, Brazil, April 2002 to August 2004: 2, percent volume of most consumed items; 3, frequency of aquatic, terrestrial, and undetermined items; 4, diet breadth by standard length classes.

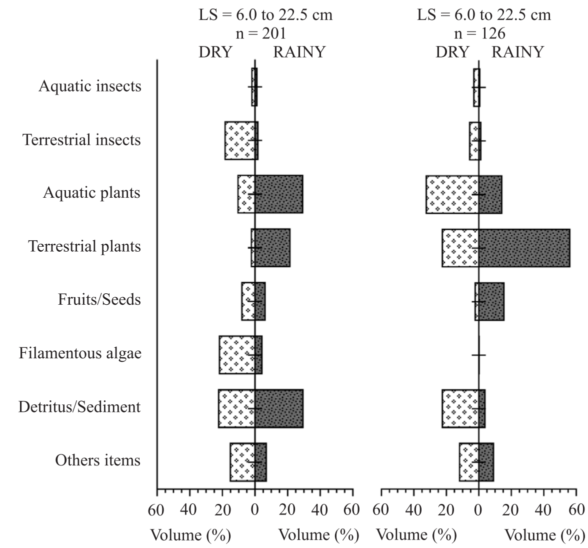


Figure 5. Percent volume of food items in the stomach of *Pterodoras granulosus* (Valenciennes, 1821) during the dry and rainy seasons by specimen standard length classes, in the Lajeado Reservoir, Tocantins, Brazil, April 2002 to August 2004 (n, number of analyzed stomachs).

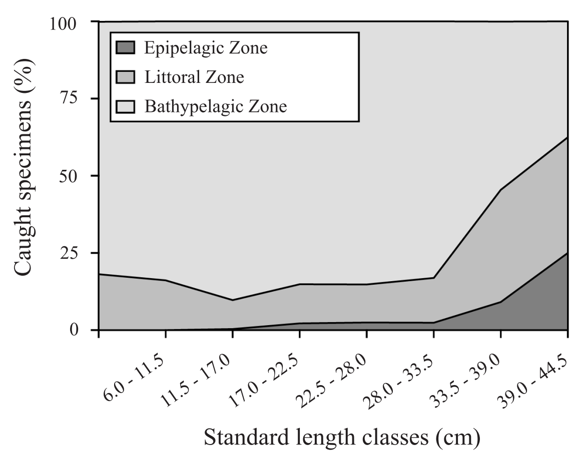


Figure 6. Frequency of caught specimens de *Pterodoras granulosus* (Valenciennes, 1821) by standard length classes and sampling site, in the Lajeado Reservoir, Tocantins, Brazil, April 2002 to August 2004 (LS, standard length average; n, number of analysed stomachs).

Comparison between the diets of small and large individuals in the two hydrological periods (dry and rainy seasons) showed that the diet of large (≥22.5 cm) and small (<22.5 cm) fish are similar in the rainy season (r_s = 0.7381, gl = 7, $p < 0.05$). During the dry season, small fish fed mainly on detritus/sediment, filamentous algae and terrestrial insects; in the rainy season, they consumed aquatic plants, detritus/sediment and terrestrial plants. In the dry season, large fish fed mainly on aquatic plants, detritus/sediment, and terrestrial plants, while plant matter (terrestrial and aquatic plants and fruit/seeds) predominated in the rainy season (Fig. 5).

Catch frequency showed that smaller fish were caught predominantly in the bathypelagic habitat. In contrast, fish larger than 28 cm were also caught in the epipelagic and the littoral habitats (Fig. 6).

DISCUSSION

The use of a wide variety of foods, including both animal and plant resources, suggest that the armado catfish is a euriphagic species with herbivorous tendency, as also reported by LAUZANNE & LOUBENS (1985), HAHN *et al*. (1992), FERRIZ *et al*. (2000), and GASPAR DA LUZ *et al*. (2002). However, it should be noted that the armado catfish showed a strong ontogenetic diet shift in Lajeado Reservoir. The percentage of detritus and sediment in the diet gradually reduced as individuals grew, while the percentage of plants, especially terrestrial ones, increased. The increasing importance of plants in the diet of large *P. granulosus*, especially terrestrial plants, resulted in a more specialized diet, as shown by diet breadth values. It is likely that small fish feed predominantly on bottom sediments, while large fish tend to explore the water surface and shallow littoral areas, in addition to deeper habitats.

The ecological importance of armado catfish as a dispersal agent of terrestrial plants was pointed out by STEVAUX *et al*. (1994) and PILATI *et al*. (1999). The most common fruit and seed in the diet of the armado catfish in the Lajeado Reservoir were goiabinha (*Psidium* sp., Myrtaceae), pimenta-de-macaco (*Xylopia* spp., Annonaceae), oiti (*Licania* spp., Chrysobalanaceae), imbaúba (*Cecropia* spp., Cecropiaceae), jenipapo (*Genipa* spp., Rubiaceae), mama cadela (*Brosimum* spp., Moraceae), casco d'anta (*Rauvolfia* spp., Apocynaceae), tarumã (*Vitex* spp., Verbenaceae), and buriti (*Mauritia* spp., Arecaceae). Although the viability of these seeds was not analyzed in this study, we observed that most seeds were morphologically intact. The high frequency of fruit and seeds in the diet of large fish may be related either to the size of the fruit (gape size limitation) or to the feeding sites used by adults. In addition to terrestrial plants, macrophytes were the predominant aquatic plant item found in the stomach of the armado catfish, especially *Utricularia* spp. (Lentibulariaceae). Even though *Utricularia* is a photosynthesizing plant, it is also behaves as an active consumer, by trapping different kinds of phyto- and zooplankton (POMPÊO & BERTUGA, 1996; ESKINAZI-SANT'ANNA *et al*., 2002). The major importance of *Utricularia* spp. in the diet of the armado, therefore, may be related to the higher proteic content available in tissues. However, the opportunistic behavior of *P. granulosus* in the use of resources (PANATTIERI & DEL BARCO, 1981; FERRIZ *et al*., 2000) indicates that the availability of this macrophyte probably determined its consumption. It is worth noting that among 69 fish species whose diets were analyzed during the first six years after the formation of the Itaipu Reservoir, only the armado catfish used macrophytes as a food source (HAHN *et al*., 1992; GASPAR DA LUZ *et al*., 2002).

Molluscs were also an important diet component, especially bivalves. Two of the species present in the stomach of the armado catfish, *Melanoides tuberculatus* (Müller, 1774) and *Corbicula largilliert* (Philippi, 1844), are invaders of the Tocantins River basin (THIENGO *et al*., 2005; ROCHA-MIRANDA & MARTINS-SILVA, 2006). Some studies point to the importance of *P. granulosus* in the control of these invasive molluscs (DARRIGRAN & COLAUTTI, 1994; MONTALTO *et al*., 1999; FERRIZ *et al*., 2000), however, the armado may also contribute dispersing *Corbicula fluminea* (Müller, 1774) to other aquatic environments (CANTANHÊDE *et al*., 2008). Considering the fact that the proliferation of these molluscs has disastrous environmental consequences, it is urgent to study their dispersal dynamics as well as the role of predatory fish in the control/facilitation of invasion processes (CANTANHÊDE *et al*., 2008).

During the dry season, the sharp drop in tributary discharge in the basin favors the formation of large backwaters and the growth of filamentous algae, which were largely consumed by small *P. granulosus* individuals. In the Itaipu Reservoir, juvenile armado catfish are found mainly in the transitional zone between the tributary and the reservoir, whereas adult armado are most often found in the reservoir main body. In these areas, juveniles feed on filamentous algae and microcrustaceans, while adults prefer macrophytes and molluscs (AGOSTINHO & JÚLIO JÚNIOR, 1999). The importance of filamentous algae in the diet of *P. granulosus* has been shown by HAHN *et al*. (1992) and GASPAR DA LUZ *et al*. (2002) as well. In the rainy season, the main dietary components of large armado in Lajeado were terrestrial plants and fruit/seeds. These items are either brought into the reservoir by rain or are directly accessible by browsing on semi-submerged vegetation of the tributaries. In the dry season, these items become less available and the individuals use aquatic plants as their main dietary resource. Lastly, it is worth noting that during the dry season, large fish showed a diet similar to small fish collected in the rainy season. This pattern suggests little temporal feeding overlap among size-classes, a behavior that weakens competitive interactions.

Many fish adjust their diets to meet their growth requirements (HAHN *et al*., 2000; ORTÊNCIO-FILHO *et al*., 2001; LIMA-JUNIOR & GOITEN, 2003) and to better exploit the availability of food resources (LOWE-MCCONNELL, 1987; ABELHA *et al*., 2001) during their lifecycles. As a result, individuals of the same species have different dietary habits as a function of spatial (AGOSTINHO *et al*., 1997; ABUJANRA *et al*., 1999) and/or seasonal (HAHN *et al*., 1997) factors. The occurrence of large *P. granulosus* in the littoral and epipelagic habitats, together with the predominance of small fish in the bathypelagic area, suggests habitat partition among size-classes. Differences in ontogenetic habitat use could be due to the improved locomotion capacity (WOOTTON, 1990) or a low predation probability when fish attain large size. Such pattern of environmental use was in accordance with the ontogenetic diet shift observed.

In short, small fish predominated in the benthic area and fed also on detritus and sediment, while large fish explored open water sites and littoral shore habitats, feeding mainly on terrestrial plants. Despite the clear herbivorous behavior reported here, reservoir aging and the consequent changes in the structure and composition of the aquatic community will likely promote gradual changes in diet composition of *P. granulosus*, as observed in the Itaipu Reservoir (GASPAR DA LUZ *et al*., 2002).

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