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Short term effects of Tucuruí Dam (Amazonia, Brazil) on the trophic organization of fish communities

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Synopsis

A dam on a river course induces numerous changes in the aquatic environment both in the newly formed reservoir and in the river downstream. These changes modify the food resources available to fishes. As a consequence, fish communities undergo rapid transformations particularly in terms of trophic organization. Tucuruí Dam, closed on the Tocantins River, Brazil, in September 1984, formed a large reservoir of approximately 2200 km^2. Analyses of fish stomach contents were performed before and after the completion of the dam in the downstream section of the river as well as in the reservoir. Resource availability was seen through the relative contribution of food items in supporting the biomass. Main changes caused by the dam consisted of an increase in fishes as a food resource and of a parallel decrease of sediment both in the reservoir and in the downstream part of the river. In addition, in the downstream section, the relative contribution of plankton as a food resource diminished after dam closure. We identified 8 feeding regimes before dam closure. From them the trophic structure of fish communities were established and compared. Most of the community biomass was from specialist feeders. Contribution of piscivores increased after closure; planktivores became unimportant after closure downstream. Some species were shown to change their diet in the transformed environments either downstream or in the reservoir. However, these changes in individual species diet did not seem to play a major role in the transformation of trophic structure of the fish communities.

Introduction

Damming a river leads to drastic changes in the aquatic environment (Balon 1974, 1978, Baxter 1977, Petr 1978, Bernacsek 1984, Junk & Nunes de Mello 1987). In the reservoir itself processes of sedimentation and stratification take place and the initial degradation of the flooded vegetation releases not only nutrients but also toxic components as for example H_2S and NH_4. In the section of the river below the dam water becomes impoverished because a great amount of organic and inorganic materials are retained in the reservoir, the natural flow regime is disturbed and geomorphological processes affect differently the substrata and the margins (Ligon et al. 1995). These modifications induce major changes in food resources available to fishes. In the river the main energy source is allochthonous organic material, whereas lakes are fundamentally autotrophic systems (Goulding 1980, Goulding et al. 1988, Araujo Lima et al. 1995). However, in the first interval of reservoir formation, there is an intense heterotrophic activity as organic matter of the inundated vegetation and flooded soil is used by organisms (Baxter 1977). In the river below a dam, the changes in food resources appear more difficult to foresee. They probably depend on a large number of parameters including retention time of water in the reservoir, amount of nutrients and flow regime. The way fish communities adapt to and utilize these new resources is poorly known and the few available results are sometimes contradictory (Ferreira 1984, Arcifa & Meschiatti 1993, Agostinho & Zalewski 1995, Araujo Lima et al. 1995).

In order to survive the major perturbation induced by the damming, fish populations face numerous challenges. In the very short term, individual fishes have to resist the adverse environmental conditions, as for example, low oxygen concentration, which is common in the first interval of reservoir formation in the humid tropic (Van der Heide 1982, Pereira 1995). They must also encounter sufficient and adequate food resources in order to fulfill their maintenance requirements. In the context of a modified environment with changing food resources, two types of situation may happen. Fishes may find in the new environment the food they are adapted to, or they may be able to change their diet according to the nature of the food present. A general assumption is that fish species, particularly Neotropical ones, are not specialized in their food regime (Knöppel 1970, Araujo Lima et al. 1995). However research works on the feeding ecology of Neotropical fishes show that very peculiar feeding adaptations to detritivory (Bowen 1983), frugivory (Goulding & Carvalho 1982), planktivory (Carvalho 1978, Carvalho 1980), scale eating (Viera & Gery 1979, Sazima 1984) exist. Moreover, Marlier (1968) considers that 18 species out of a total of 41 analyzed from a floodplain lake of Central Amazon are specialist feeders.

In that context this study aims at describing the changes in trophic structure of fish communities in a large river transformed by a hydroelectric dam in relation to the changes in resources availability. In addition, we evaluate the impact of modifications in individual species' diet on the changes in trophic structure.

Materials and methods

Site description

The present research was undertaken in the lower part of the Tocantins River, which flows into the southern arm of the Amazon estuary near the town of Belém (Figure 1). At approximately 400 km upstream from the river mouth, a huge hydroelectric dam has been built and closed in September 1984. The Tocantins River is typical of large Amazonian rivers, with an extension of 2500 km, a drainage area of about 767 000 km^2 and a mean annual discharge of ca. 10 000 $m^3 s^{-1}$. The dam formed a large reservoir of more than 2200 km^2.

From 1980 to 1982, prior to the Tucuruí Dam closure, considerable ecological work was done on fish communities living in the Lower Tocantins River (Santos et al. 1984, Mérona 1985, 1986, Carvalho & Mérona 1986, Mérona et al. 1987). Data showed that the region housed a very diverse fish fauna. From experimental gillnet fishing, almost 300 fish species of adult size larger than 10 cm SL, have been recorded in a section of about 400 km long.

Sampling

Sampling was made by means of fleet of gillnets. A fleet consisted of 11 nets with mesh size 15, 20, 25, 30, 35, 40, 45, 50, 55, 60 and 70 mm between adjacent knots. In the pre-closure period, two batteries were used whereas, because of material restrictions, only one was used in the post-closure period. Nets were set before sunset at 18:00 h and left in the water until 18:00 h of next day, with visits at 22 h, 6 h and noon. They were placed in marginal biotopes with low current. In the pre-closure period, between July 1980 and July 1982, sampling took place twice a year, in November, at the end of low water period and in July, at the beginning of the flood. These periods were chosen in order to take into account the seasonality in resource availability and resource use by fishes (Prejs & Prejs 1987). The first period corresponds to the end of the high water period, which can be considered as the growing season for fish. The other is the beginning of the flood where numerous species start the process of maturation taking advantage of the new resources brought by the rising of the waters. In addition, similar water level in these two periods provides comparable experimental fishing conditions. After the closure, because the environment shows very rapid changes, sampling was done every other month from November 1984 to November 1987.

In the pre-closure period, 4 stations, distributed along the course of the lower Tocantins, were visited: Acari-Pucu and Icangui in the section downstream of the dam, and Breu Branco and Jatobal in the section corresponding to the reservoir (Figure 1). In the post-closure period, the same stations downstream were sampled, and the two stations upstream were substituted by 5 stations in the reservoir at different distances from the dam. Overall there are 10 samples before dam

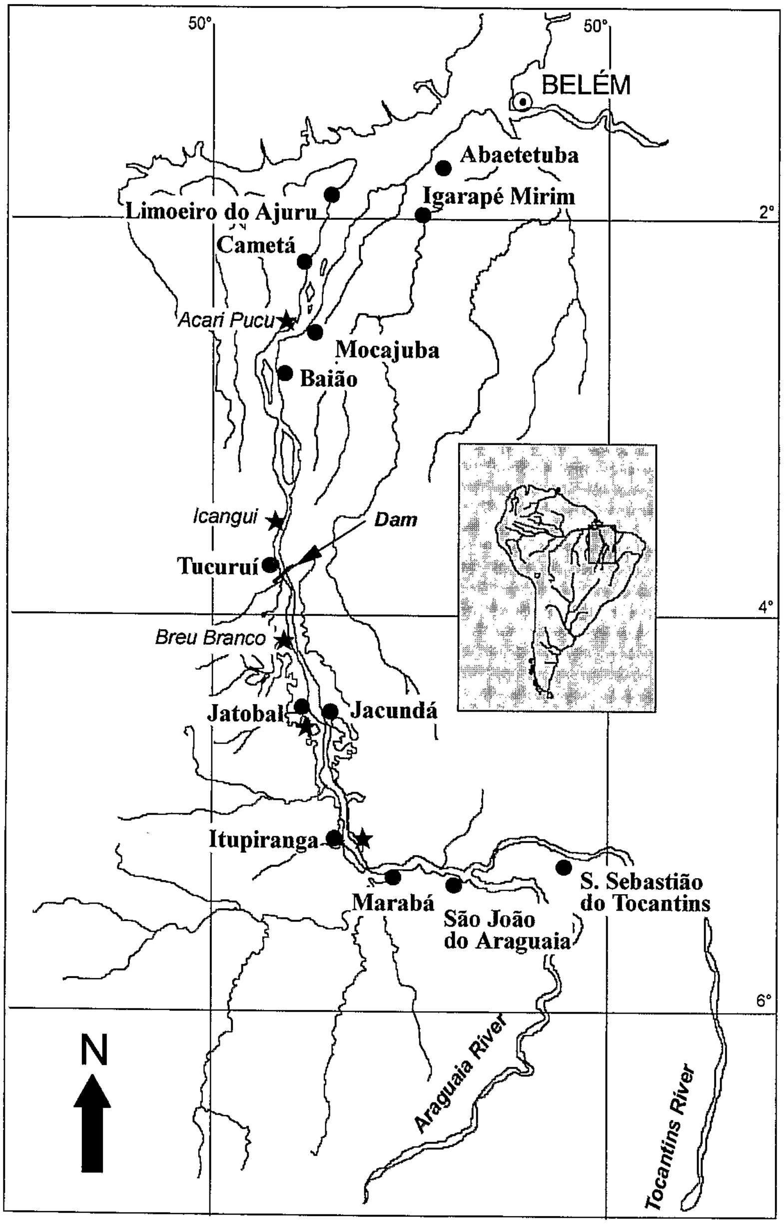

Figure 1. Geographical situation of the study site. The asterisks indicate the experimental fishing stations.

closure in each of the sections, 22 samples downstream and 44 samples in the reservoir after the dam closure.

Food habit studies

Immediately after the capture, fish specimens were identified to the species level, counted, measured for standard length to the nearest 1 mm and weighted. Representative specimens of all species were kept in the systematic collection of INPA. Species names are those used in Santos et al.(1984) except for some groups where revisions were published between the field work and this publication. These groups are: genus *Serrasalmus* (Jegu & Santos 1988), family Anostomidae

(Santos & Jegu 1989), genus *Pterygoplichthys* (Weber 1991, 1992), family Curimatidae (Vari 1989, 1992a,b), and genus *Cichlasoma* (Kullander 1983). Because of the great number of species in the samples and the difficult field conditions in the tropics, the priority in collecting the stomachs was given to species with a variable and diversified feeding regime. For these species, whenever available, 10 adult specimens of each species from each sample were dissected and their stomach collected and kept in alcohol for further analysis in the laboratory. When the number of specimens of a species in the sample was >10, a subsample of 10 was taken at random. In the laboratory, the whole contents were spread in a Petri dish and all individual items separated. Seven main items were recognized: terrestrial invertebrates, aquatic invertebrates other than decapods and plankton, vegetal material, fish, decapods, plankton, and detritus. The invertebrates' categories included mainly insects but occasionally mollusks, worms, sponges, etc. The detritus category included all kind of fine material from the bottom, mud, organic pellicle and sediment in general. The vegetal material category included any kind of higher plant parts such as leaves, fruits, seeds and wood but also a few filamentous algae. Decapods encountered are mainly shrimps but occasionally small crabs. The volumetric importance of each item was estimated and a score between 1 and 5 was attributed so that the total of scores equalized 5 for a stomach. The mean score for all the individuals of each species was computed and transformed into a percentage.

Some species captured are known, from the literature and from personal observations on central Amazonian floodplain, to eat only one kind of food in any habitat where they were investigated (specialist feeder). These species were included in the analysis with a regime consisting in 100% of the unique food item. This is the case of (1) large piscivores (*Brachyplatystoma flavicans*, *B. filamentosus*, *B. vaillanti*, *Phractocephalus hemiliopterus*, *Paulicea lutkeni*, *Boulengerella maculata*, and *Hoplias malabaricus*), (2) detritivores (*Ancistrus* spp., *Hypostomus* spp., *Pterygoplichthys* spp., *Panaque nigrolineatus*, *Curimata* spp., and *Curimatella* spp.), and (3) herbivores (*Myleus* spp.). Data for these species can be found in Marlier (1968), Knöppel (1970, 1972), Saul (1975), Goulding (1980), Novoa and Ramos (1982), Power (1983), Ferreira (1984), Goulding et al. (1988), Braga (1990), Flecker (1992), Araujo-Lima et al. (1995), Planquette et al. (1996), Hahn et al. (1998).

Data treatments

For each sampling operation, capture data were expressed in gram of fish of each species for 1100 m^2 of net and 24 h of fishing. In order to evaluate the resources availability in the environment, we estimated, for every sample, the relative abundance of each item in the environment by the part of the entire community biomass supported by that particular item (Winemiller 1989). Following the line of arguments presented by this author, this method avoids the risk of underestimate resources from undersampled fish microhabitats and overestimate resources actually invulnerable to predation by fishes. The method is evidently more reliable when based on very diverse communities containing many ecomorphotypes, which is the case in the Tocantins River. For each of the data sets, the captured biomass of each species was split into the different food items according to their percentage in the stomachs. The sum, for the entire species list, of the biomass supported by each food item gives an indication of their relative availability in the environment for a particular sample. Differences in the pattern of resource availability were tested by a two-way analysis of variance (SYSTAT® 9) after homogenization of variances by a log-transformation.

To determine the feeding regime, species were separated in feeding groups according to the percentages of each food item in their stomachs. A hierarchical procedure was realized in 8 steps:

Step 1: >70% of detritus	detritivore
Step 2: >70% of plankton	planktivore
Step 3: >70% of fish	piscivore
Step 4: >70% of superior plant material	macrophytophage
Step 5: >70% of food of animal origin and >70% of invertebrates	invertivore
Step 6: >70% of food of animal origin and >70% of invertebrates	unspecialized carnivore
Step 7: >70% of food of vegetal origin	unspecialized vegetarian
Step 8: none of the above statements	omnivore

The trophic structures of communities were established by summing the captured biomass of species pertaining to each of the feeding groups. Differences in trophic structures were tested by a two-way analysis of variance (SYSTAT® 9) after homogenization of variances by a log-transformation.

Species with more than 2 specimens analyzed for their stomach content were selected for individual diet change analysis after dam closure.

Results

In the pre-closure period, 3809 stomachs belonging to 99 species were analyzed (Appendix 1). During this period, between June 1980 and July 1982, total capture included 144 species downstream and 152 upstream. After addition of specialist feeders not observed on the field, the numbers of species included into the analysis were, respectively, 103 and 99 and these species represented altogether 95.4% of the total biomass downstream and 94.5% of the total biomass upstream.

In the post-closure period 962 stomachs belonging to 77 species in the downstream section and 1670 stomachs from 63 fish species in the reservoir were analyzed (Appendix 2, 3). In this period 141 species were captured in the downstream section and 127 in the reservoir. After addition of specialist feeders not observed in the field, the numbers of species included in the analysis were 88 and 75, respectively. These species represented 95.4% of the biomass in the downstream section and 95.6% in the reservoir.

Food resource availability

Figures 2a,b,c show the resources availability based on biomass distribution into the food items before and after dam closure in the two sections of the river. Resource availability was statistically different in the two sections considered before the closure ($p < 0.001$). The main differences were a much higher contribution of fish and a much lower contribution of plankton in the upstream section. Also detritus were of less importance in the upstream than in the downstream section.

After closure of the dam, in the downstream section as well as in the reservoir, there was a significant difference in resource availability between before and after the closure ($p = 0.022$ and $p = 0.014$, respectively). In both sections, the main differences were a considerable increase in the relative importance of fish as a food resource and a decrease of detritus resource. The importance of plankton diminished downstream

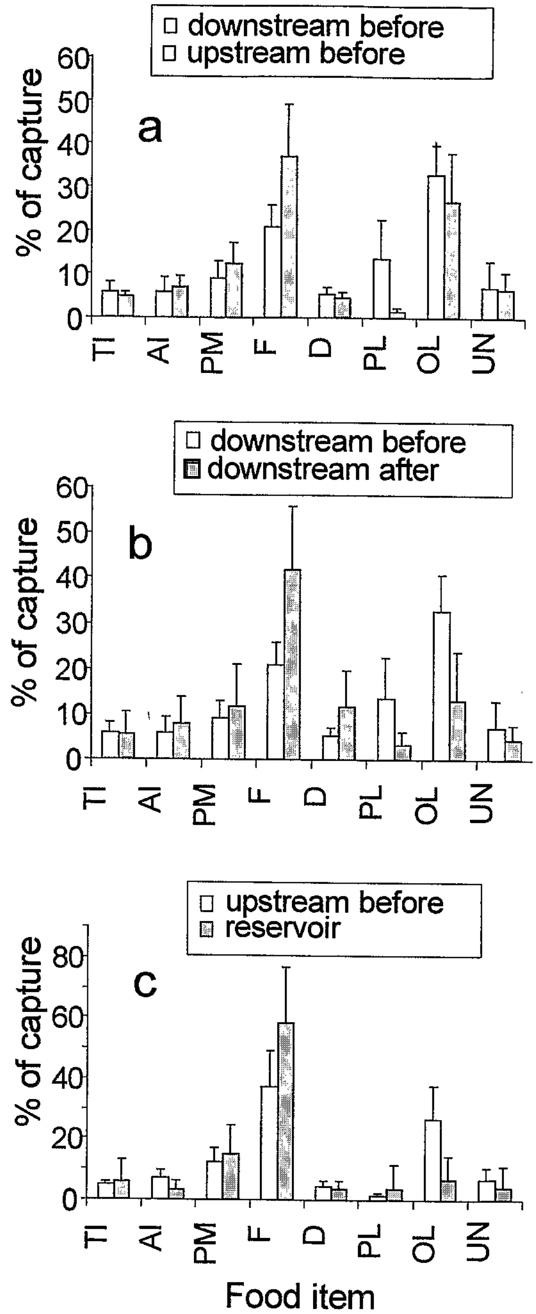

Figure 2. Relative availability of food resources as indicated by fish biomass supported by each of the considered item: a – downstream and upstream sections before dam closure, b – downstream section before and after dam closure, c – upstream section before dam closure and reservoir (TI = terrestrial invertebrates, AI = aquatic invertebrates, PM = plant material, F = fish, D = decapod, Pl = plankton, OL = organic layer, UN = unknown).

where decapods, mainly shrimps, were more readily available. In the reservoir a slight increase of plankton and a reduction of aquatic invertebrates was registered.

Determination of feeding groups and trophic structures

Among the 8 groups determined by the hierarchical procedure adopted, 5 can be considered as groups of specialist feeders (consuming almost exclusively one food item). These are the detritivores, planktivores, piscivores, macrophytophages and invertivores. These groups include 65 of the 99 analyzed species. The 3 other groups are generalist feeders. Carnivores prey upon fish associated with insects or decapods. Vegetarians consume algae, superior plant elements and benthic organic layer. Omnivores mix animal and vegetal food. The generalists represent only 34 of the analyzed species.

The trophic structures of fish communities in the two sections of the river and in the two periods show the great dominance of specialist feeders (Figures 3a,b,c). Nonetheless the two sections had different structures ($p < 0.001$). Detritivores, piscivores, and planktivores formed together most of the biomass downstream before the damming when upstream only the two first groups are dominant. There were significant changes in trophic structure after the closure downstream ($p < 0.001$) and in the reservoir ($p = 0.001$). The relative contribution of piscivores increased downstream to the detriment of detritivores and planktivores. In that same section carnivores and macrophytophages also saw their contribution increased. In the reservoir piscivores represented almost 50% of the community biomass so that the other groups had a very low contribution to the trophic structure. However, a high variability between samples in the relative contribution of piscivores is observed.

Changes in individual species' diet after the closure of Tucuruí dam

Downstream of the dam only 46 species were analyzed both in the pre- and post closure period but these species represent more than 70% of the captured biomass. Nineteen of them showed a change in their diet (Table 1). Despite the low number of specimens analyzed for some species, a few general tendencies could be detected.

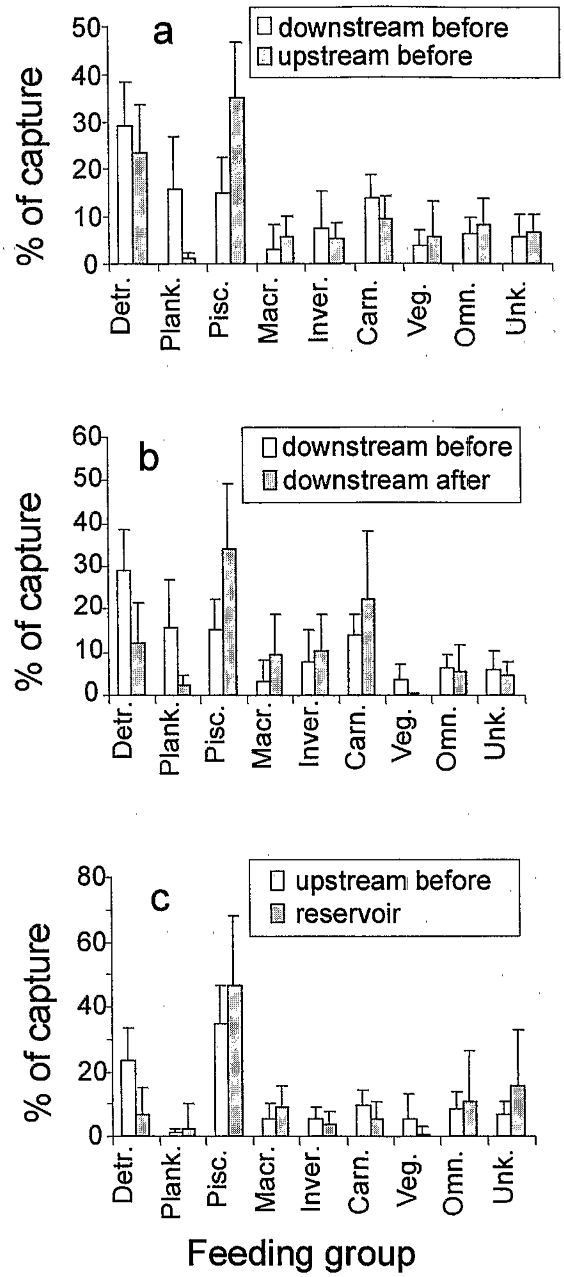

Figure 3. Trophic structure of fish communities as indicated by relative biomass of each of the feeding groups: a – downstream and upstream sections before dam closure, b – downstream section before and after dam closure, c – upstream section before dam closure and reservoir (Detr. = detritivores, Plank. = planktivores, Pisc. = piscivores, Macr. = macrophytophages, Inver. = Invertivores, Carn. = unspecialized carnivores, Veg. = unspecialized vegetarians, Omn. = omnivores, Unk. = unknown).

Table 1. Changes in the diet of some species after dam closure in the downstream section compared to the corresponding section before closure.

Species	Nb analyzed	Group before	Nb analyzed	Group after
Hemiodus unimaculatus	241	Detritivore	8	Macrophytophagous
Anchovia surinamensis	15	Planktivore	17	Unspecialized carnivore
Laemolyta petiti	38	Macrophytophagous	17	Unspecialized vegetarian
Geophagus jurupari	9	Invertivore	14	Omnivore
Agoniates anchovia	59	Unspecialized carnivore	25	Piscivore
Sorubim lima	13	Unspecialized carnivore	19	Piscivore
Ageneiosus brevifilis	8	Unspecialized carnivore	14	Piscivore
Lycengraulis batesii	114	Unspecialized carnivore	12	Piscivore
Pinirampus pirinampu	13	Unspecialized carnivore	12	Piscivore
Acestrorhynchus microlepis	8	Unspecialized carnivore	10	Piscivore
Cynodon gibbus	12	Unspecialized carnivore	5	Piscivore
Pimelodus blochii	6	Unspecialized carnivore	3	Piscivore
Oxydoras niger	5	Unspecialized vegetarian	8	Invertivore
Hemiodus argenteus	75	Unspecialized vegetarian	7	Macrophytophagous
Triportheus angulatus	59	Omnivore	17	Unspecialized carnivore
Pimelodella cristata	5	Omnivore	12	Unspecialized carnivore
Piaractus brachypomus	3	Omnivore	7	Macrophytophagous
Geophagus surinamensis	35	Omnivore	4	Detritivore
Leporinus affinis	70	Omnivore	3	Piscivore

Table 2. Changes in the diet of some species after dam closure in the reservoir compared to the upstream section before closure.

Species	Nb analyzed	Group before	Nb analyzed	Group after
Hemiodus unimaculatus	241	Detritivore	26	Omnivore
Myleus pacu	132	Macrophytophagous	40	Unspecialized vegetarian
Triportheus albus	285	Invertivore	44	Unspecialized carnivore
Auchenipterus nuchalis	196	Invertivore	16	Unspecialized carnivore
Geophagus jurupari	9	Invertivore	7	Omnivore
Acestrorhynchus microlepis	8	Unspecialized carnivore	67	Piscivore
Ageneiosus brevifilis	8	Unspecialized carnivore	18	Piscivore
Cynodon gibbus	12	Unspecialized carnivore	5	Piscivore
Lycengraulis batesii	114	Unspecialized carnivore	4	Piscivore
Hemiodus argenteus	75	Unspecialized vegetarian	43	Macrophytophagous
Triportheus angulatus	59	Omnivore	32	Unspecialized carnivore
Argonectes scapularis	12	Omnivore	32	Invertivore
Leporinus friderici	51	Omnivore	7	Macrophytophagous
Geophagus surinamensis	35	Omnivore	7	Unspecialized carnivore
Triportheus elongatus	169	Omnivore	5	Unspecialized carnivore
Mesonauta festivum	4	Omnivore	5	Invertivore

The more common change downstream was a tendency towards specialization. Number of unspecialized carnivores shifted to a regime almost exclusively constituted of fish and 5 omnivores turned to consume preferentially food either of animal or vegetal origin.

In the reservoir the same tendency towards a specialization was present but to a lesser extent. Of the 48 species analyzed, 16 appeared to change their diet and 5 of them diversified their food (Table 2). The other 11 shifted from an unspecialized carnivore diet to a piscivore (4 species), from an unspecialized vegetarian diet to a macrophytophagous (1 species), or from an omnivore diet to more specialized (6 species).

The contribution of these changes to the trophic structures of the communities appeared to be very low (Figure 4). Altogether, the contribution of the species considered to have changed their feeding behavior formed 20% of the total biomass downstream and 11% in the reservoir. Moreover, although important changes were observed in groups of low representation, the

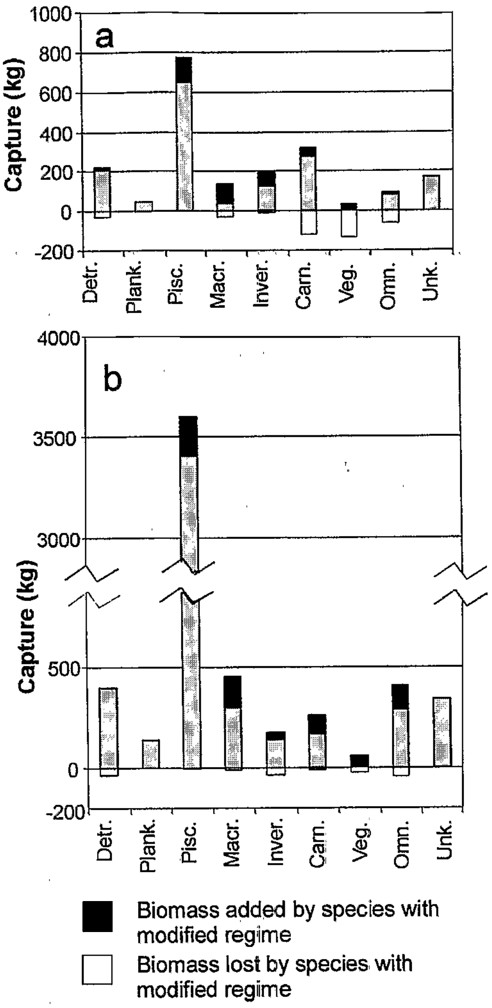

Figure 4. Relative contribution of species having suffered a change in diet in the trophic structures: a – downstream, b – reservoir (same legend as in Figure 3).

general pattern of the trophic structures was not greatly influenced by the biomass of these species. For example, the percentage of biomass added to the dominant group of piscivores by former unspecialized carnivores was as low as 16% in the downstream section and 5.5% in the reservoir.

Discussion

Resources availability

Before the dam closure the main differences observed in resources available to fishes in the two sections of the river were the greater availability of fish prey and the very low contribution of plankton in the upstream section as compared to the downstream section. The great availability of fishes in the upstream part could be explained by the migrating movements of numerous fish species in Amazonian rivers. Reproductive migrations are notorious in Neotropical fishes although poorly known in detail (but see Petrere 1985). In rivers without extensive floodplains, which is the case of the lower Tocantins, a general hypothesis is that migrating species move upstream in large concentrations to reproduce, whereas juveniles are drawn passively downstream (Godoy 1959, 1967, Bayley 1973, Paiva & Araujo Bastos 1982). Data from commercial fisheries in the Tocantins seem to corroborate this hypothesis (Carvalho & Mérona 1986). Adult fish concentrations in shoals during the upriver migration as well as the abundance of juveniles in the waterway after the reproduction make fishes more vulnerable to predation. Fishes become a more available food resource. The absence of plankton in the upstream section was apparently due to the strong current always present in that part of the river. Conversely, the downstream section flows through an alluvial plain. The river is wide with a relatively low current and plankton is abundant enough to sustain large populations of planktivores (Carvalho et al. 1978, Carvalho 1978).

The changes observed in resource availability are consistent with the transformations in the aquatic environment associated with dam closure. Downstream, the water released from the reservoir becomes impoverished in nutrients because of the sedimentation processes in the lake (Baxter 1977, Ward & Stanford 1989, Gore 1994). As a result, the production of organic benthic layer and plankton must decrease, at least until large populations of plankton develop in the lake. Unexpected, on the other hand, was the large increase in fishes as a fish food resource. Usually the closure of a dam suppresses the flood during the filling of the reservoir and regulates it afterwards. By diminishing the extension of flooded areas downstream, this flood control affects the reproduction of numerous fish species which eventually serve as prey for piscivores (Balon 1974, Welcomme 1979, Ponton & Vauchel 1998). However, increases in piscivore species populations have been recorded downstream from dams, especially in stretches close to the dike where fishes feed upon migratory species blocked by the dam (Sagua 1978). It is then probable that this increase of availability of fishes as a food resource originates more from their vulnerability than from the absolute abundance of prey species.

In the reservoir, our results show that the dominance of fishes as a food resource increased. The explosive development of some fish populations in the first years following reservoir filling is a well-known phenomenon (Balon 1974, Petr 1975, Goldsmith & Hildyard 1984). Initial continuous inundation of terrestrial areas provides abundant food resources and shelter to juveniles. This is in part responsible for the explosive development of an abundant food resource (Adiase 1969, Lowe-McConnell 1973, Lelek & El Zarka 1973, Petr 1975). Another main feature of change in resource availability in the reservoir as compared to the river was the relative decline of the benthic organic layer. In large impoundments set in forested areas, the bottom becomes totally anoxic due to the decomposition of the large amount of submerged plants and a large part of the benthic resources becomes inaccessible to fishes. Unexpectedly, plankton did not seem to have a significant role as a resource, although other studies show that they develop rapidly in reservoirs from very scarce populations in the rivers (Fernando 1994), a fact that was also observed in Tucuruí Reservoir (Tundisi et al. 1993). Evidently, in order that plankton be a resource for fish communities, some planktivorous species must be present in the community. In the lower Tocantins such species exist. One of these is the mapara, *Hypophtalmus marginatus*, but it has been shown that this species, prior to dam construction, was limited to the section downstream from the future dam location (Carvalho & Mérona 1986). Another is *Anodus elongatus*, which originally had a wider distribution but did not develop in the lake until the end of our investigation in 1987.

Trophic structure

The present study shows that patterns of community trophic structure were similar to those of resource availability. This means that the main bulk of biomass in the communities was formed by specialist species, those that consume almost exclusively one kind of food. This observation disagrees with the assumption that Neotropical fishes are generally opportunist feeders (Araujo-Lima et al. 1995). This does not mean that the number of food specialist species is larger than the number of generalist. Many species present in the lower Tocantins communities were not analyzed in this study and it is likely that most of them are generalist because we included known specialists in the analysis. For example, a number of cichlids have been already reported to be omnivores (Ferreira 1981, Santos 1991). The only conclusion is that, in the biotopes studied here, these generalist species did not have a high contribution in biomass to the community. Conversely, in small Amazonian streams, generalist species are dominant (Knöppel 1970, Saul 1975). The influence of habitat on the trophic structure of fish communities has not been much studied but Angermeier and Karr (1983) were able to demonstrate an increase of the number of food specialist with stream size in a tropical stream in Panama. The hypothesis is that when the river widens and deepens the number of niche increases and the environment is more stable, allowing the development of more specialist fish populations (Lowe-McConnell 1987).

We show that, before dam closure, food specialist species were mainly detritivores and piscivores, but also planktivores in the downstream section. However, unspecialized carnivores represented about 10% of the biomass. Most of these latter species consumed large quantities of shrimp whose great abundance has been reported in a parallel study (Odinetz-Collart 1991). In Amazonian waters, a number of species consume shrimp and some of them present morphological adaptations for shrimp predation but none of them can be considered as exclusive shrimp eaters (Goulding & Ferreira 1984).

After dam closure, the piscivores formed the group that took most advantage of the increase of the prey fish food resource in both sections, whereas the biomass of unspecialized carnivores seemed to follow the increase in relative abundance of decapods. In the reservoir the trophic structure appeared to be unbalanced with piscivores making up almost 50% of the biomass. This dominance of piscivores in the newly formed impoundments has already been reported in many situations in South America (Leentvaar 1973, Vieira 1982, Alvarez et al. 1986, Hahn et al. 1998). This phenomenon however does not seem to occur in all tropical reservoirs. In 4 of the large reservoirs in tropical Africa, piscivores were never dominant, although their abundance increased after the filling (Evans & Vanderpuye 1973, Van der Lingen 1973, El-Zarka 1973, Balon 1974). Development of piscivores must depend on the composition of the riverine ichthyofauna and the growth parameters of these species. Another notable modification in the reservoir following dam closure was the reduction of the relative contribution of two of the generalist species groups. Really, the fact that benthic and marginal resources became scarce in relation to the lake size resulted in the shift of generalist species towards the most abundant and available resource.

Changes in individual species diet

Few of the species considered as specialists in the pre-closure period changed their diet after the closure. Among them *Hemiodus unimaculatus*, which consumed more than 82% of unidentifiable benthic organic material in the first period, shifted to a macrophytophagous regime downstream and consumed also plankton in the reservoir. Like its sister species *Hemiodus argenteus*, this species is most probably an omnivore who is able to change its alimentary source with the available resources (Ferreira 1984, Planquette et al. 1996). In a detailed study of these species in Curuá-Una Reservoir, Holanda (1982) distinguished 8 different items in the stomach contents. Among them, higher plant remains were of significant importance. A similar change from food specialist to generalist could be noted for *Geophagus jurupari*, which shifted from an invertivorous regime before dam closure to omnivorous habits afterwards. The opportunistic nature of the feeding behavior of *Geophagus* species is attested by data from a central Amazon floodplain lake (Honda 1972) and the Rio Negro (Ferreira 1981, Goulding et al. 1988) where very heterogeneous diets, variable in time and in place, were observed. Another interesting case is that of *Anchovia surinamensis*, a small engraulid inhabiting the lower course of rivers, which is morphologically adapted to planktivory with long and tight gill rakers. In the downstream section after the closure of the dam, when plankton became scarce, this species was able to consume fishes despite its small size. Paradoxically, in the same conditions, *Triportheus angulatus*, which is a typical omnivore surface feeder as shown by previous studies in Madeira River and central Amazon floodplain (Goulding 1980, Almeida 1984), consumed plankton. The case of such a switch is also known for an African species (*Alestes baremoze*), being exclusively planktivore in Lake Chad and invertivore in rivers (Lauzanne 1976).

These few cases excepted, the changes observed in individual species diets were not dramatic. A lot of unspecialized carnivores, who took advantage of shrimp abundance in the pre-closure period, tended to consume more fishes after dam closure both downstream and in the reservoir. Shrimp consumption by Amazonian fishes is well known and Goulding & Ferreira (1984) list 50 species which have been reported to eat shrimp. However none of them appears to be shrimp eating specialists. Even *Sorubim lima* and *Plagioscion* spp. which eat shrimps as a major part of their diet in various environments (Annibal 1982, Novoa & Ramos 1982, Goulding & Ferreira 1984) seem to be more benthic feeders than shrimp feeders. As for the omnivores, they shifted from one to another available resource as circumstances presented.

The great adaptability of generalist species should give them a competitive advantage in the case of rapid changes in the environment. This did not, however, seem to be the case in the Tocantins situation. The contribution of such species in the overall pattern of trophic structure appeared to be very low. This situation is probably due to the presence of a large number of piscivores in the river ichthyofauna, which were able to develop rapidly and control the abundance of generalist species. Today, Brazilian law requires power companies to construct fish culture stations in order to stock the reservoir with those species prevented from entering the reservoir from downstream. Given the great development of piscivores in Tucuruí Reservoir, the efficiency of such a measure is dubious.

The main cause of modifications in trophic organization by Tucuruí Dam then seemed to be the changes in abundance of specialist fishes. Evidently this conclusion is only valid in the limits of this study, i.e. an extremely diverse fish fauna in the river before the dam and short-term post-closure effects.

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Appendix 1. Results of stomach contents analysis prior to the closure of Tucuruí Dam.

Species	Capture down-stream (g)	Capture upstream (g)	Nb. analyzed	Terr. invert.	Aqua invert.	Plant mater.	Fish	Decapod	Plankton	Organic layer
Acestrorhynchus falcatus	169	0	3				100.00			
Acestrorhynchus falcirostris	15858	0	2				100.00			
Acestrorhynchus microlepis	29144	1003	8	18.56		19.59	61.86			
Achirus achirus	3199	238	1							100.00
Acnodon normani	0	532	2	25.00		75.00				
Ageneiosus brevifilis	11009	12452	8	8.67		11.22	22.96	56.63		
Ageneiosus dentatus	3290	1472	24	1.41	1.41	1.69	25.99	69.49		
Ageneiosus ucayalensis	19090	6070	63	17.28	8.39	2.89	35.62	29.41	2.14	2.14
Agoniates anchovia	965	1106	59	51.11	3.19	0.22	44.93			
Anchovia surinamensis	7830	0	15				2.98		96.78	
Anodus elongatus	210378	16650	126	1.73	0.58	6.07	1.34		77.31	12.99
Argonectes scapularis	1600	5253	7	26.97	33.42	19.93				19.93
Auchenipterichthys longimanus	10101	1534	87	51.37	25.43	6.70	1.30		2.00	13.20
Auchenipterus nuchalis	65181	27521	196	31.90	41.72	11.43	2.20	4.40	5.82	2.53
Bivibranchia protractila	0	5263	2							100.00
Boulengerella cuvieri	27018	134107	97	4.02		2.61	91.37	2.01		
Brycon carpophagus	2471	590	22	48.18	8.88	37.65				5.29
Bryconops alburnoides	5839	0	9	77.77	1.46	8.75			8.02	4.01
Centromochlus heckelii	4	1311	7	58.46	15.24		10.00			16.50
Chalceus macrolepidotus	4608	1275	17	53.44	33.26	12.68	0.61			
Cichla cf. monoculus	7555	19458	17			12.82	87.18			
Cichla temensis	2922	7132	2				60.61	39.39		
Curimata cyprinoides	112946	110692	284		0.50	0.90	2.10			96.50
Curimatella alburna	5300	265	4							100.00
Curimatella dorsalis	2598	734	20						0.63	99.37
Curimatella immaculata	7382	114	14				4.59		13.44	81.97
Cynodon gibbus	3415	2948	12	3.20	9.14	8.31	64.94	14.29		
Cyphocharax microcephalus	353	97	2			1.00				99.00
Cyphocharax plombeus	732	397	8				0.80		1.20	98.00
Cyphocharax spilurus	257	685	2							100.00
Eigenmannia virescens	341	21	1		66.67					33.33
Geophagus jurupari	3925	775	9	2.67	83.33	4.00	3.75			6.00
Geophagus surinamensis	11663	11288	29	1.80	39.09	29.98	4.93		0.64	23.56
Glyptoperichthys joselimaianus	449	217	2							100.00

Appendix 1. Continued.

Species	Capture down-stream (g)	Capture upstream (g)	Nb. analyzed	Terr. invert.	Aqua invert.	Plant mater.	Fish	Decapod	Plankton	Organic layer
Hassar wilderi	15085	8671	12	0.52	49.35	10.78		1.82	4.68	32.86
Hemiancistrus vittatus	489	1486	3						2.78	97.22
Hemiodus argenteus	33570	25755	75		4.28	32.24	1.48		4.93	57.07
Hemiodus unimaculatus	53577	36234	241		2.07	11.66	1.17		0.78	82.90
Hemisorubim platyrhynchos	1454	11532	3			22.92	77.08			
Holobrycon pesu	16	625	14	54.67	9.43	35.90				
Hoplias malabaricus	10094	3914	4				100.00			
Hydrolycus scomberoides	14650	139601	59	2.02		0.30	89.60	4.04		4.04
Hypophthalnus marginatus	9108	0	24						91.18	8.82
Hypostomus emarginatus	11833	59484	10		7.12	9.51	0.57		2.37	80.43
Hypostomus sp. 1	1781	76	11				3.67			96.33
Laemolyta petiti	15231	7466	38		12.58	77.37				11.05
Leporinus affinis	2863	36469	70		50.86	25.17	6.11	9.49	2.46	5.92
Leporinus friderici	1771	5641	51	10.76	4.04	58.76	8.19	7.18		10.92
Leporinus pachycheilus	35	2747	1			100.00				
Leporinus trifasciatus	613	704	3		50.00	50.00				
Lycengraulis batesii	17553	413	114	6.44		0.21	45.01	47.92	0.42	
Megalodoras irwini	0	2059	4		10.00	90.00				
Mesonauta festivus	66	0	4	17.75	17.75	48.39				16.13
Moenkhausia grandisquamis	41	128	4	60.94		39.06				
Moenkhausia jamesi	23	71	1	100.00						
Myleus micans	102	2210	47	3.44	0.49	90.80	0.10			5.17
Myleus pacu	18597	13328	132	5.50	9.03	75.40	1.37		0.50	7.45
Myleus rubripinnis	198	0	4	1.25	1.25	97.50				
Myleus schomburgkii	0	9499	6	5.15		92.78				2.06
Myleus sp.	11418	6698	4	3.75	3.75	92.50				
Mylossoma duriventre	4124	408	12	13.79		86.21				
Osteoglossum bicirrhosum	6726	14674	13	31.62	46.71	11.56	9.56			0.56
Oxydoras niger	1284	31409	5		17.65	14.12				68.24
Pachypops furcraeus	250	0	13	14.86	53.14		7.00			25.00
Pachypops sp.	3040	8553	5	12.32	75.67		8.46			3.56
Pachyurus schomburgkii	1260	3551	4	33.28	66.72					
Parauchenipterus galeatus	5002	1691	93	26.86	6.93	43.83	9.48	11.90		0.81
Paulicea lutkeni	0	38140	1				100.00			
Pellona castelnaeana	24008	8480	20		2.00		98.00			
Piaractus brachypomus	695	412	3			66.63	33.25			
Pimelodella cristata	680	503	5		7.00	30.00	63.00			
Pimelodina flavipinnis	1178	1177	10		7.00		93.00			
Pimelodus blochii	2431	7925	6	28.01	6.44	18.43	45.78			1.33
Pinirampus pirinampu	12847	22928	13				66.60	33.30		
Plagioscion squamosissimus	62241	49025	83	6.59	0.51	2.69	54.84	34.73	0.65	
Pristigaster cayana	1773	1803	30	31.50	27.71	9.21	20.79		2.36	8.43
Prochilodus nigricans	32804	30367	94							100.00
Psectrogaster amazonica	164611	42506	229	0.40		2.00	0.80		0.40	96.15
Pseudoplatystoma fasciatum	7942	9579	1	14.25	14.25		71.46			
Pterengraulis atherinoides	11043	31	55	8.04			82.47	8.76		0.52
Ramphichthys rostratus	202	2369	1			20.00				80.00
Retroculus lapidifer	0	10865	5							100.00
Rhaphiodon vulpinus	13046	66159	106	7.32	0.24	2.13	90.10	0.21		
Roeboides thurni	645	299	4	21.15	21.15		57.69			
Schizodon vittatus	5620	6560	39			75.16	3.48		1.37	19.88

Appendix 1. Continued.

Species	Capture down-stream (g)	Capture upstream (g)	Nb. analyzed	Terr. invert.	Aqua invert.	Plant mater.	Fish	Decapod	Plankton	Organic layer
Semaprochilodus brama	18323	5210	37			1.00	1.50		0.80	96.70
Serrasalmus calmoni	1191	0	1			12.85	87.15			
Serrasalmus eigenmanni	797	497	20			3.26	96.74			
Serrasalmus geryi	11	0	1				100.00			
Serrasalmus nattereri	12371	3511	35		3.18	5.68	84.09	3.41	3.41	
Serrasalmus rhombeus	9200	45060	114	4.74		10.72	79.12	4.85		0.56
Sorubim lima	1173	12707	13		3.61	24.30	40.96	31.12		
Sternopygus macrurus	0	92	1		25.00	25.00				50.00
Sternopygus obtusirostris	303	110	1	50.00	50.00					
Tocantinsia piresi	0	5514	5	21.88		46.88	31.25			
Triportheus albus	10977	7631	385	55.32	15.15	20.53	2.28	1.94	2.17	2.62
Triportheus angulatus	32597	14384	59	34.80	25.76	33.11	0.22		4.78	1.33
Triportheus elongatus	7484	7619	169	28.10	6.73	56.18	1.80		6.52	0.67
Utiaritichthys sennaebragai	997	20209	17	2.35		96.47				1.18
Total capture	1256636	1227969								

Appendix 2. Results of stomach contents analysis after closure of Tucuruí Dam in the downstream section.

Species	Capture (g)	Nb. analyzed	Terr. invert.	Aqua invert.	Plant mater.	Fish	Decapod	Plankton	Organic layer
Acestrorhynchus falcatus	2262	5				100.00			
Acestrorhynchus falcirostris	37387	20				90.00	10.00		
Acestrorhynchus microlepis	11984	10				90.00	10.00		
Ageneiosus dentatus	39586	32		35.94		26.56	37.5		
Ageneiosus ucayalensis	29030	23		4.35		43.48	52.17		
Ageneisosus brevifilis	17119	14				100.00			
Agoniates anchovia	24606	25	4.00			96.00			
Anchovia surinamensis	3982	17		5.88		64.71		29.41	
Anodus elongatus	23309	3						100.00	
Auchenipterichthys longinmanus	8936	32	81.88	7.19			10.94		
Auchenipterus nuchalis	54845	11	61.36	34.09	4.55				
Biotodoma cupido	465	3			33.33				66.67
Boulengerella cuvieri	4039	7				100.00			
Brachyplatystoma flavicans	18505	2				100.00			
Bryconops alburnoides	1626	1	100.00						
Caenotropus labyrinthicus	2044	4							100.00
Cetopsis sp.	1812	2				100.00			
Charax gibbosus	385	1				100.00			
Cichla cf. monoculus	18254	9				88.89	11.11		
Cichla temensis	13363	12				100.00			
Curimatella alburna	7907	1							100.00
Curimatella dorsalis	1568	1							100.00
Curimatella immaculata	3975	4							100.00
Cynodon gibbus	2436	5		5.00		95.00			
Cyphocharax microcephalus	1839	4							100.00
Cyphocharax plombeus	2746	4							100.00
Geophagus jurupari	11010	14		62.86					37.14

Appendix 2. Continued.

Species	Capture (g)	Nb. analyzed	Terr. invert.	Aqua invert.	Plant mater.	Fish	Decapod	Plankton	Organic layer
Geophagus surinamensis	16502	4		12.50					87.50
Hassar wilderi	18745	12		36.25				16.67	47.08
Hemiodus argenteus	62755	7			92.86				7.14
Hemiodus unimaculatus	34443	8			87.5				12.5
Hemisorubim platyrhynchos	4091	2				100.00			
Hoplias malabaricus	157365	22		1.14		89.77	9.09		
Hydrolycus scomberoides	89450	10				100.00			
Hypophthalmus marginatus	13834	13						100.00	
Hypoptopoma sp.	9208	1							100.00
Laemolyta petiti	30032	17			41.18				58.82
Leporinus affinis	3731	3				100.00			
Leporinus friderici	28406	49		3.67	60.51	35.82			
Loporinus trifasciatus	356	2			100.00				
Loricariichthys nudirostris	9480	11							100.00
Lycengraulis batesi	21632	12		8.33		91.67			
Mesonauta festivus	479	1	100.00						
Metinis hypsauchen	6818	37						100.00	
Myleus micans	2128	2			100.00				
Myleus torquatus	837	1			100.00				
Mylossoma duriventre	6200	1			100.00				
Oxydoras niger	70378	8		100.00					
Pachypops sp.	3726	6		100.00					
Pachyurus schomburgki	5597	1		100.00					
Parauchenipterus galeatus	28348	17	23.24	0.29	64.71		11.76		
Pellona castelnaeana	59884	9				100.00			
Pellona flavipinnis	5756	2				100.00			
Phractocephalus hemiliopterus	11765	1				100.00			
Piaractus brachypomus	2748	7			85.71	14.29			
Pimelodella cristata	2741	12		35.42		56.25	8.33		
Pimelodus blochii	3538	3				100.00			
Pinirampus pirinampu	21684	12				83.33	16.67		
Plagioscion squamosissimus	184128	87	1.15	3.45		50.57	44.83		
Plagioscion surinamensis	6977	13				15.38	84.62		
Prochilodus nigricans	15201	13							100.00
Psectrogaster amazonica	119089	68							100.00
Pseudoplastystoma fasciatum	27005	8				100.00			
Pterengraulis atherinoides	12124	9				33.33	66.67		
Pterodoras granulosus	2881	2			50.00	50.00			
Rhaphiodon vulpinus	79411	64		1.56		85.94	12.5		
Schizodon vittatus	29715	5			100.00				
Semaprochilodus brama	35229	15			6.68				93.33
Serrasalmus calmoni	773	3			100.00				
Serrasalmus eigenmanni	659	4			25.00	75.00			
Serrasalmus gibbus	205	2				100.00			
Serrasalmus nattereri	62172	46				97.83	2.17		
Serrasalmus rhombeus	18172	20				95.00	5.00		
Sorubim lima	17879	19				89.47	10.53		
Triportheus albus	50739	8	75.63	6.25	18.13				
Triportheus angulatus	40372	17	8.82	23.53	17.65	2.94		47.06	
Triportheus elongatus	23161	2				100.00			
Total capture	1985462								

Appendix 3. Results of stomach contents analysis after closure of Tucuruí Dam in the reservoir.

Species	Capture (g)	Nb. analyzed	Terr. invert.	Aqua invert.	Plant mater.	Fish	Decapod	Plankton	Organic layer
Acestrorhynchus falcatus	3900	1				100.00			
Acestrorhynchus falcirostris	11721	2				100.00			
Acestrorhynchus microlepis	30072	67	1.49	4.18	0.37	90.97	2.99		
Ageneiosus dentatus	2569	7		57.14		42.86			
Ageneiosus ucayalensis	3100	25		69.20		26.80	4.00		
Ageneisosus brevifilis	153967	18				100.00			
Agoniates anchovia	7749	17	11.76	41.18		47.06			
Anchovia surinamensis	5501	11		9.09				72.73	18.18
Anodus elongatus	137860	90	3.33					96.39	0.28
Argonectes scapularis	32549	32	2.34	80.94					16.72
Auchenipterus nuchalis	11156	16	21.88	32.81		20.31		25.00	
Boulengerella cuvieri	195635	92		1.14	3.21	91.30	4.35		
Brycon carpophagus	71711	50	32.70	3.50	54.30	9.50			
Bryconops alburnoides	43	6	66.67	33.33					
Cichla cf. monoculus	252862	17				94.12	5.88		
Cichla temensis	233195	29				86.21	13.79		
Cynodon gibbus	3884	5		20.00		80.00			
Geophagus jurupari	5528	7		56.43	7.86				35.71
Geophagus surinamensis	17070	7		50.00	10.71	28.57			10.71
Hassar wilderi	611	1		100.00					
Hemiodus argenteus	139602	43		8.72	88.95			1.16	1.16
Hemiodus unimaculatus	117251	26		3.85	49.04	7.69		36.54	2.88
Heros severum	3355	2		50.00	50.00				
Hydrolycus scomberoides	862602	112				99.11	0.89		
Hypoptopoma sp.	1533	5							100.00
Laemolyta petiti	34640	40		3.13	75.00	5.00			16.88
Leporinus affinis	34728	39	0.64	41.67	34.49	17.56	2.56	3.08	
Leporinus friderici	17136	7			85.71	14.29			
Lycengraulis batesi	9774	4		1.25		98.75			
Mesonauta festivus	736	5	100.00						
Myleus pacu	62063	40	7.50		69.38	18.75		1.88	2.50
Myleus schomburgki	12192	19			77.63	5.26			17.11
Myleus sp.	344	13		12.31	87.69				
Myleus torquatus	858	5			100.00				
Mylossoma duriventris	772	4		25.00	75.00				
Osteoglossum biccirhosum	139408	10	75.00			25.00			
Parauchenipterus galeatus	93337	23	50.43		49.57				
Pellona castelnaeana	51762	6				83.33	16.67		
Piaractus brachypomus	35581	32	7.81	15.00	49.53	24.22	3.13		
Pimelodella cristata	2293	1				100.00			
Pinirampus pirinampu	23289	1				100.00			
Plagioscion squamosissimus	131452	25				56.00	44.00		
Poptella orbicularis	50	4		100.00					
Prochilodus nigricans	168509	109			2.06				97.94
Psectrogaster amazonica	8022	28							100.00
Pseudoplastystoma fasciatum	15030	4				75.00	25.00		
Pterengraulis atherinoides	3050	2		50.00		50.00			
Rhaphiodon vulpinus	190511	79	0.63	1.90	0.63	77.22	19.62		
Schizodon vittatus	215134	82	0.61	0.06	94.94			1.16	3.23
Semaprochilodus brama	220405	123			17.89				82.11
Serrasalmus calmoni	876	2				100.00			

Appendix 3. Continued.

Species	Capture (g)	Nb. analyzed	Terr. invert.	Aqua invert.	Plant mater.	Fish	Decapod	Plankton	Organic layer
Serrasalmus eigenmanni	1034	3				100.00			
Serrasalmus gibbus	515197	4				100.00			
Serrasalmus nattereri	252163	33	2.42		9.70	84.85			
Serrasalmus rhombeus	772694	75		2.60		94.73	2.67		
Serrasalmus spilopleura	19605	37	0.68	3.51	4.73	91.08			
Sorubim lima	45786	31		57.26		16.94	25.81		
Tocantinsia piresi	20239	5	1.00		60.00	20.00		19.00	
Triportheus albus	29512	44	35.23	7.95	29.55	27.27			
Triportheus angulatus	15727	32	67.34	0.16	18.44	14.06			
Triportheus elongatus	17097	5	59.00			21.00	20.00		
Utiaritichthys sennaebragai	32433	3	8.33		91.67				
Total capture	5840506								