

# THEORETICAL RESERVOIR ECOLOGY AND ITS APPLICATIONS

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## **PATTERNS OF COLONIZATION IN NEOTROPICAL RESERVOIRS, AND PROGNOSSES ON AGING**

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### **ABSTRACT**

We review patterns of reservoir colonization and aging in neotropical reservoirs, with emphasis on the Upper Paraná River Basin, Brazil. The filling stage was a period of rapid and intense transformation, an abrupt transition from a lotic to a lentic environment. This stage lasted 8-80 d, which was relatively short in comparison with reservoirs in temperate zones or other reservoirs in the Amazon basin. Release of nutrients, increases in water transparency, decreases in turbulence, and development of thermal and oxygen stratification were key factors characterizing this transition. Anoxic events were critical during this stage. During the first few days individuals of various fish species occupied the entire reservoir and water column, independent of the habitat they had inhabited in the river, or the type they would eventually inhabit in the new lake. As anoxia progressed, fish moved to the embayments and tributaries including the main river. Species that remained in the reservoir concentrated mainly in shallow, littoral areas and near the mouth of tributaries. The season of the filling stage was extremely relevant to the colonization process. The ecological transformations observed during the filling stage of neotropical reservoirs are likely more accentuated than in temperate reservoirs, because water temperature remains warm around the year.

After the original upsurge, no severe changes in abiotic environment were identified, but a gradual colonization by submersed aquatic macrophytes was evident in some reservoirs, and changes in the fish communities were identified in all reservoirs. In one reservoir, diversity of macrophyte communities became higher than in natural environments within its basin. There was a general absence of fish species pre-adapted to colonize the pelagic zones, and species diversity was higher in the littoral zone. Many species that colonized neotropical reservoirs reproduced in lateral tributaries or upstream stretches. In at least one reservoir, reproductive effort by the fish assemblage in the first two years was low and increased thereafter. Migrators and large-bodied fish reached peak abundance shortly after impoundment, but assemblages shifted towards a

dominance by sedentary, medium-sized species. As stability was approached after the upsurge period, diets shifted towards more stable, autochthonous resources. In general, detritivores-illophages showed sharp reductions, whereas herbivores and zooplanktivores increased. Piscivores increased in some reservoirs but decreased in others; often they became abundant where pre-adapted lacustrine species existed within the basin.

Anticipated environmental changes such as reservoir age, including nutrient accumulation, siltation, and habitat deterioration, particularly in the littoral zone are expected to cause faster changes in the fish assemblages. The most notable ones include a reduction in the number of top predators, mean size of species, and species richness. Pelagic species are expected to become dominant as benthic organisms decline and littoral habitat deteriorate. Short-lived species with fast growth or reproductive compensation are expected to have survival advantages. In advanced stages of aging, fish communities are anticipated to consist of species typical of murky, shallow water, with low oxygen. These aging effects are long-term, but will become noticeable in littoral areas sooner.

*Key words:* fish colonization, limnology, trophic upsurge, aquatic macrophytes, aging, neotropical reservoirs.

## INTRODUCTION

An unavoidable effect of impoundment on the aquatic fauna and flora is a shift in species composition and abundance, with extreme proliferation of some species and reduction, or even elimination, of others. This impact is greatly influenced by characteristics of the biota, such as reproductive strategies, migratory patterns and trophic specialization, and of the reservoir itself (e.g., morphology, hydrology). Presence of other reservoirs in the watershed, design and operational characteristics of the dam, uses of the watershed (e.g., forestry, agriculture, urbanization), geology, and various interactions among these variables are also important.

Colonization of a newly-formed impoundment depends on the biota present in the riverine and lacustrine environments of the pre-impoundment basin. Colonization occurs during a period dominated by heterotrophic conditions induced by the flooding and by the subsequent decomposition of terrestrial organic matter (Margalef, 1983). These conditions last as long as the inundated organic matter drops to a mineralization threshold. During this period, large portions of the reservoir, especially in deep layers and near the dam, support only anaerobic life.

Details of events that follow this initial heterotrophic period are unpredictable. Generally, the responses of the communities to subsequent perturbations, whether natural or manipulated, are incomplete because the perturbations are further modified before the fish communities can fully respond. The result is a chaotic succession of reactions marked by a reduction in the interdependence among species, and a lower biotic stability, deranging continuity of the biota and natural succession processes (Wetzel, 1990). These conditions limit organisms that participate in this rapid initial succession to those with broad physiological tolerance-and behavioral plasticity.

The responses of aquatic fauna to hydrological modifications induced by dams are not well understood within the neotropical faunal realm (Nelson, 1994), despite intensive

damming. Our current insights are handicapped by the limited amount of knowledge accumulated about the structure and function of riverine communities, and about the evolution of these communities once the reservoir is impounded. Conceivably, this undesirable state of knowledge could be reversed by a well organized sequence of investigations, along with long-term monitoring and adaptive management experiments, based on clear and concise objectives. Such a venture might better delineate the actions needed to mitigate impacts of reservoir construction on the aquatic biota and fishery yield.

A major impact of the reservoir is to reduce the cyclicality of the riverine environment. Reservoir operations alters, eliminate, or restrain natural hydrologic cycles. Also, the biota in the reservoir basin become subject to non-cyclic perturbations related to operation of the dam, exacerbating the instability induced by the foreign environment. The biotic community responds by reducing its species diversity, becoming gradually simpler, a response most clear during the first few years after impoundment. The low fish species richness and the reduced importance of the fishery in reservoirs of the Paraná River Basin are the results of this process (Agostinho, 1994). These responses are prompted by catalysts such as unsuitable water temperature, low dissolved oxygen, low habitat diversity, inadequate or restricted spawning sites, absence of suitable prey during at least one stage of ontogeny, absence of shelter for prey (O'Brien, 1990), and exclusion through interspecific interactions (Paller & Gladden, 1992). Moreover, some fish respond very quickly to impoundment, whereas others respond gradually over years or decades, according to their trophic nature.

We use available data and literature to review patterns of reservoir colonization and aging in neotropical reservoirs. Emphasis is placed on information from the Upper Paraná River Basin, in particular Itaipu Reservoir because it boasts the longer series of data available among South American reservoirs, especially its ichthyofauna. We separate our commentary into two broad divisions: the filling stage, and the colonization stage. Next, we consider potential responses to aging. Throughout the text, the basin of reservoirs and rivers is identified only if it is not the Upper Paraná River Basin. Fish community assessments were made with gill nets and herein termed experimental fishery to distinguish them from commercial fishery.

### THE FILLING STAGE

We define the filling stage as the period beginning with the closure of the dam and ending when the reservoir reaches normal operation. This period can last from a few days (e.g., 8 d for Caxias Reservoir) to a few weeks (e.g., 80 d for Corumbá Reservoir). These periods are relatively short in comparison with those in temperate zones and the Amazon Basin, essentially because neotropical reservoirs of the Upper Paraná River are built mainly for hydropower production, and are thus located where natural discharges are high. Length and timing of the filling stage can have a significant impact on reservoir colonization. Below we describe the abiotic environment during the filling stage, and its interactions with the fish community in the reservoir basin.

#### The Abiotic Environment

Information about the changes that occur during the filling stage of neotropical reservoirs are scarce because much of the monitoring is conducted by hydroelectric

companies, who emphasize the post-impoundment stage when hydropower generation occurs, although, conditions during the filling stage provide a peculiar view of the biotic community. The filling stage is characterized by intense ecological change, the transformation of a terrestrial environment into an aquatic one.

The rapid transformations observed after filling begins result partially from an increase in retention time, because a lotic environment is suddenly converted into a lentic one. When a reservoir is formed, vertical patterns associated with thermal stratification, influencing nutrient cycling and the distribution of organisms, are added to the longitudinal patterns predominant before. Increases in nutrient concentrations are usually registered during the filling stage (Esteves, 1988; Matsumura-Tundisi *et al.*, 1991; Patterson *et al.*, 1997). Increases can be attributed to releases from litter decomposition and from flooded soils and terrestrial vegetation (Matsumura-Tundisi *et al.*, 1991). The effect of nutrient releases that start influencing the reservoir during the filling stage can be observed long after filling, especially in deeper water layers where elevated nutrient concentrations and high electrical conductivity have been recorded (Thomaz *et al.*, 1997a). The thermal and oxygen stratification that follows the reservoir formation plays an important role in extending the accumulation of ions to the post-filling stage, especially in reservoirs with a surface outflow.

Patterns of anoxia may vary with the characteristics and density of the inundated terrestrial vegetation, morphology of the basin, and duration of the filling stage. During the filling of Corumbá Reservoir, which flooded an area of savannah, the anoxic layer remained about 10 m below the surface (De Filippo *et al.*, 1997). In contrast in Samuel Reservoir (Amazon River Basin), which flooded rain forest, the anoxic layer reached down to about 6 m below the surface (Matsumura-Tundisi *et al.*, 1991).

Despite high nutrient concentrations during and soon after filling, the concentration of key elements such as phosphorus is influenced by antagonistic processes. Thus, while nutrient releases are high, the lentic characteristics of the new environment encourage sedimentation, causing loss of phosphorus and other nutrients to anaerobic sediments. Nevertheless, nutrient accumulation in the water during the filling stage suggests that input of nutrients from the flooded areas is high during this period, maintaining the water-sediment equilibrium at a high level. After the filling stage, the water-sediment equilibrium shifts to a lower level, often limiting availability of phosphorus and other nutrients in the water.

Increases in retention time and nutrient concentrations indicate that the filling stage is favorable to primary producers, such as phytoplankton and aquatic macrophytes. In Corumbá Reservoir phytoplankton production in the subsurface layer was less than  $0.2 \text{ mgO}_2 \text{ L}^{-1} \text{ h}^{-1}$  on day 10 after the dam was closed, but increased to over  $0.8 \text{ mgO}_2 \text{ L}^{-1} \text{ h}^{-1}$  by day 39 (Thomaz *et al.*, 1997b). This strongly suggests that the filling stage is followed by a period of rapid eutrophication. Along with increases in nutrient levels there was a decrease in light attenuation (measured as photosynthetically active radiation – PAR that changed from  $4.60 \text{ m}^{-1}$  at day 1 of filling to  $0.89 \text{ m}^{-1}$  by day 10 (Thomaz *et al.*, 1997b). This increased clarity is partly associated with sedimentation of inorganic particles and flocculation of colloidal particles, prompted by the high levels of organic matter.

Marked decreases in dissolved oxygen are another common occurrence during the filling stage. Oxygen can be virtually absent from part or the entire water column. During

the filling stage, anoxia is independent of seasonal climatic factors, and dictated mainly by decomposition of the particulate and dissolved organic matter derived from flooded terrestrial biomass (Esteves, 1988). Results from Tucuruí Reservoir indicate that it takes ten years after filling to complete the decomposition of the inundated forest. There are reports of anoxia during the filling stage of reservoirs in regions covered by tropical forests with high biomass (Matsumura-Tundisi *et al.*, 1991), but in savannah regions with lower biomass levels as well (De Filippo *et al.*, 1997). Anoxic events are very important during the formation of reservoir ecosystems because they can negatively affect survival and thereby the diversity of the aquatic fauna.

The rapid oxygen consumption which follows the filling stage is instigated by the mineralization of labile dissolved compounds released through leaching of the flooded organic matter. The oxygen consumption is sustained by decomposition of the more refractory material, represented especially by the particulate fraction. Microcosm experiments suggested that the oxygen demand by dissolved organic matter is considerably higher than the demand generated by particulate organic matter (Bianchini & Toledo, 1998).

The high input of dissolved organic matter is also responsible for the immediate increase of bacterial production during the filling stage. Also, much of the carbon flux to secondary producers originates from allochthonous inundated matter rather than from autochthonous production (Paterson *et al.*, 1997). Thus, besides contributing to increased primary production by phytoplankton and aquatic macrophytes, the input of terrestrially-originating detritus also contributes to increased biological activity during the filling of a reservoir.

Reduced dissolved oxygen during the filling stage changes ionic ratios and concentrations. Ions that occur predominantly in oxidized states (characteristic of rivers) are substituted by reduced forms. With regard to inorganic nitrogen, for instance, N-nitrate is substituted by N-ammonium that becomes highly concentrated (Esteves, 1988; Matsumura-Tundisi *et al.*, 1991; Thomaz *et al.*, 1997c).

Based on these observations we consider the filling stage as a period of rapid and intense transformations, an abrupt transition from a lotic to a lentic environment. Releases of nutrients, increases in water transparency, decreases in turbulence, and development of thermal stratification are key factors in this transition. The ecological transformations observed during the filling stage of neotropical reservoirs seem more accentuated than in temperate reservoirs considering that water temperature remains warm all year.

### **The Fish Community**

Reservoir filling and the physical, chemical and biological alterations associated with filling have implications for the colonization of the new environment by the ichthyofauna, but for neotropical reservoirs this process has rarely been documented. Data from a monitoring study during the filling of Salto Caxias Reservoir in Iguaçú River (FUEM/NUPELIA/COPEL, 1998b), showed that during the first few days individuals of various species occupied the entire reservoir and water column, independently of the habitat type they inhabited in the riverine environment, or the

type they would eventually inhabit in the new lacustrine environment. During this stage, the experimental fishery yielded high catch rates, suggestive of intense fish movements.

The increase in the size of anoxic volume that progresses from the bottom near the dam towards incoming streams normally occurs after about two weeks into the filling stage. It coincides with massive displacements of fish into the arms and tributaries including the main river (FUEM/NUPELIA/COPEL, 1998b). Species that remain in the reservoir concentrate mainly in shallow, littoral areas and near the mouth of tributaries (Fernando & Holčík, 1991; Rodríguez Ruiz, 1998). Wind, rain or atmospheric thermal variations (cold fronts) may promote mixing of the water column, leading to local, sometimes extensive fish kills (Tundisi *et al.*, 1993; FUEM/NUPELIA/FURNAS, 1998). The beginning of releases from the reservoir brings a new period of instability, whose magnitude and impact on species remaining in the reservoir depend on whether water is withdrawn from the surface or bottom.

The season during which filling occurs is extremely relevant to the colonization of the new reservoir environment. This is particularly true when the dam is positioned within a stretch of river crucial to the migration of potamodromous fishes. When Itaipu Reservoir was impounded in November 1982, it flooded Sete Quedas Falls, which were the upper boundary of the distribution of the migratory fish of the Middle Paraná River. When the falls were flooded, migratory species trapped between the dam and the falls dispersed into the Upper Paraná River. Among the 86 fish species recorded in Itaipu Reservoir, at least 13 had their distribution limited to the Middle and Low Paraná River and now gained access to the Upper Paraná River. Most of these species are nonmigratory, and the migrators begin their movements early in spring (Agostinho *et al.*, 1992). *Hypophthalmus edentatus* and *Pterodoras granulosus* are among the three most important in the commercial fishery. *Auchenipterus nuchalis*, *Raphiodon vulpinus*, and *Serrasalmus marginatus* are abundant in the experimental fishery. Sixteen other species remained downstream of the dam as demonstrated by sampling the stretch immediately below Itaipu Dam (Agostinho *et al.*, 1993a; Agostinho *et al.*, 1994a). Most of them exhibit migratory movements that begin in late spring and early summer. Thus, timing of the Itaipu Dam closure had a great influence on the composition of the ichthyofauna in the reservoir.

### THE COLONIZATION STAGE

We define the colonization stage as the period beginning right after the filling stage, and lasting approximately 15 years, representing the length of the data set available for Itaipu Reservoir. Below we describe spatial and temporal patterns of colonization, focusing on the ichthyofauna but including the abiotic environment and aquatic macrophytes.

#### Spatial Patterns in the Colonization by the Fish Fauna

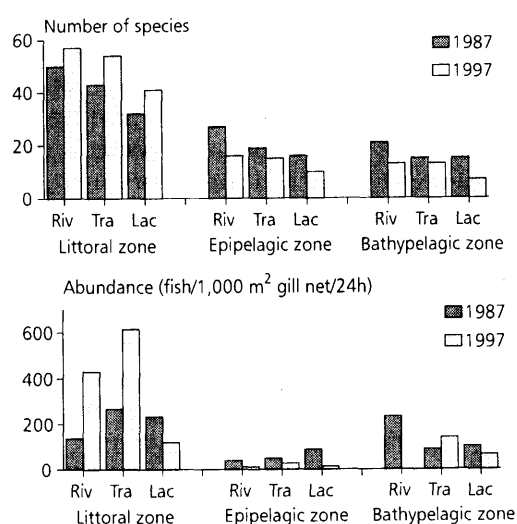
The occupation of a reservoir may be viewed as colonization or simply a major restructure in the local fish community. How the occupation is viewed will depend on the limitations imposed by the physical and chemical conditions during the heterotrophic



filling stage. The species that successfully occupy the new reservoir environment should be able to develop adaptations different from those they displayed in the lotic environment (Kubečka, 1993).

To describe the colonization process we distinguish strata oriented longitudinally (riverine, transitional, and lacustrine zones), latitudinally (littoral and pelagic), and vertically (epipelagic and bathypelagic) relative to the main axis of the reservoir, particularly in large reservoirs. In general, local species are more successful in the colonization of the riverine and littoral zones of reservoirs. The riverine zone, although not with the highest fish density or biomass (Kimmel *et al.*, 1990), often has the highest species diversity (i.e., number of species; Figure 1). The riverine zone of Itaipu Reservoir includes all the species that occur in the transitional and lacustrine zones, plus species typical of lotic stretches upstream (Agostinho & Julio, 1993). This tendency for higher species diversity in the riverine zone was evident by the second year of impoundment in Segredo Reservoir (Iguaçu River) (Agostinho *et al.*, 1997a). Higher diversity in this zone is likely due to the retention of characteristics of the original lotic environment.

On a transverse and vertical basis, the littoral zone has higher species diversity and is more productive than the epipelagic or bathypelagic zones. Productivity is associated with inputs of nutrients and food from riparian areas, by low reservoir depth, and by increased habitat structure and diversity. These differences tend to be accentuated by reservoir age (Figure 1). Fifteen years after the filling of Itaipu Reservoir, 64 out of 67 species were caught in gill nets in the littoral zone. In the epipelagic and bathypelagic zones, 20 and 22 species were found, respectively. Number of individuals caught per 1,000 m<sup>2</sup> of net during 24 h were 388 in the littoral, 22 in the epipelagic, and 20 in the bathypelagic zone.



**Figure 1** Spatial and temporal variation-in species diversity and abundance of fish species in Itaipu Reservoir. Riv = riverine, Tra = transitional, Lac = lacustrine zones.

In general, colonization of the littoral zone is by species with generalist adaptations and a wide tolerance of habitat variation. The littoral zone is often the most productive in reservoirs. In the temperate latitudes of the European continent it is inhabited mainly by cyprinids and percids, and in North America by cyprinids, silurids, and percids (Fernando & Holčík, 1991). In African reservoirs the littoral zone is occupied largely by cichlids. In Itaipu Reservoir, cichlids are also restricted to the littoral zone, but represented only 13% of the experimental fishery in 1997. An introduced sciaenid, small characoids and small siluroids dominate the littoral zone of Itaipu Reservoir.

The ichthyofauna of the Upper Paraná River lacks lacustrine endemic species that spend their entire life cycles in lentic habitats, in the sense of Fernando & Holčík (1991). In addition to the absence of natural lakes in the Paraná River Basin, the lacustrine environments of the floodplain of the river do not have species that depend exclusively on lentic environments. However, some of the endemic species are often abundant in lagoons and channels of the floodplain. Notable among these are erithrinids, callichtids, serrasalmids, and some curimatids and loricarids (Agostinho & Julio Jr, 1994). They occupy bottom habitats or have a close relation with the floating macrophytes of the littoral zone, but they do not inhabit the pelagic zones.

The absence of species pre-adapted to colonize the pelagic zones may explain the low fisheries yield in reservoirs of the Upper Paraná River. Fernando & Holčík (1991) indicated that the pelagic habitats is the most extraordinary characteristic of large impoundments, and that absence of endemic species from these habitats is the cause of low fishery yield. Fish species that occupy pelagic habitats, unlike those that occupy littoral habitats, require specific morphological and behavioral adaptations for feeding, spawning, movement, and predator avoidance. In Itaipu Reservoir, all species collected in the pelagic zones also occurred in the littoral zone. Some however, succeeded in the pelagic zones, such as the filter-feeder (mainly zooplanktivore) *H. edentatus*, the insect-zooplankton feeder *A. nuchalis*, and the piscivore *R. vulpinus*. All have adaptations in body shape, position of the mouth, and orientation of the eyes that allow them to seek pelagic prey (Freire, 1997). But although they were common in the pelagic zones, they were more abundant in the littoral zone. These three species originated from the Middle Paraná River, and occur between Itaipu and Jupia dams, including the two reservoirs upstream Itaipu (Rosana in Paranapanema River and Porto Primavera in Paraná River) constructed after Itaipu and Jupia dams were closed. The piscivorous *Plagioscion squamosissimus* (introduced) and the omnivorous *Pterodoras granulosus* are also abundant in the pelagic zones, but not as abundant as in the littoral zone. *P. squamosissimus* is the most important species in the commercial (artisanal) fisheries of almost all reservoirs of the basin (Agostinho, 1994). In African and North American reservoirs clupeids are dominants in the pelagic fauna. In temperate reservoirs of higher latitudes, osmerids and coregonids are important (Fernando & Holčík, 1991).

The bathypelagic zone is poorly inhabited, possibly dictated by factors such as thermal and oxygen stratification, density currents, food availability, and light attenuation (Matthews *et al.*, 1985; Rudstam & Magnuson, 1985; Fernando & Holčík, 1991). Like in the epipelagic zone, species diversity and fish abundance in the bathypelagic zone decreases relative to the littoral zone (Figure 1). In Itaipu Reservoir, after 15 years of

impoundment, catches in the experimental fishery in the pelagic zone (top 60 m of the water column) were dominated by the doradid *P. granulosus* (54%), followed by the loricarid *Loricariichthys* sp. (19%) and the sciaenid *P. squamosissimus* (17%).

## Temporal Patterns

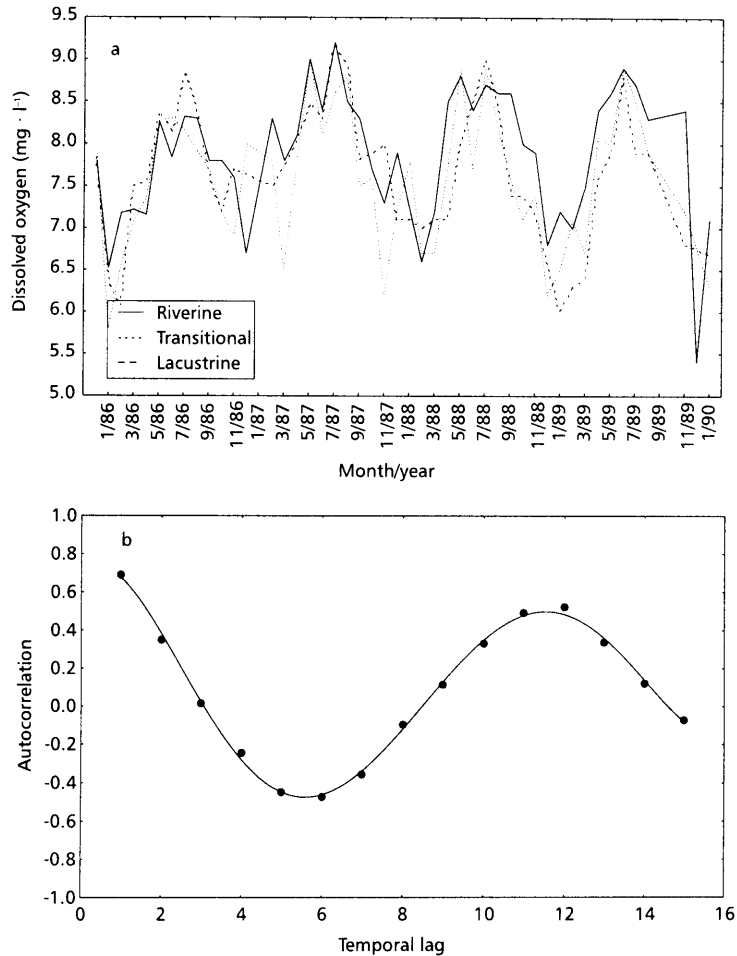
### *The Abiotic Environment*

The effects of impoundment on structural and functional characteristics of lotic ecosystems can be established by monitoring studies of the “before-after intervention” type, considering that the dam is an abrupt and permanent intervention. However, as previously recognized, few studies have evaluated the long-term effects of impoundment in neotropical reservoirs. In fact, after the initial drastic changes (see Filling Stage) the effects of increase in age require an analysis of long time-series data. Nevertheless, the influence of multiple factors, such as hydrodynamic processes resulting from the operation of the dam, coupled with the presence of temporal lags, limit the ability of time series to decipher the time dynamics characteristic of many reservoir variables.

A key aspect of the studies on temporal dynamics of limnological variables is the search for the main forces that determine the observed variability patterns. Seasonal patterns, for example, are difficult to observe when obscured by operation of the dam (Tundisi *et al.*, 1993) and releases from reservoirs upstream (Straškraba, 1990; Straškraba *et al.*, 1993). Therefore, long-term trends and abrupt changes are the patterns most readily detectable.

Seasonal and annual trends of temperature, dissolved oxygen, total phosphorus, total nitrogen, nitrates and turbidity were analysed for Itaipu Reservoir. Beside temperature, only dissolved oxygen (Figure 2a) showed a clear seasonal pattern, as identified by temporal autocorrelation analysis (Figure 2b). Maximum dissolved oxygen concentrations ( $9.0 \text{ mg} \cdot \text{L}^{-1}$ ) were occurred in winter (June-July), whereas minimum concentrations ( $5.5\text{-}6.5 \text{ mg} \cdot \text{L}^{-1}$ ) occurred in summer (January-February).

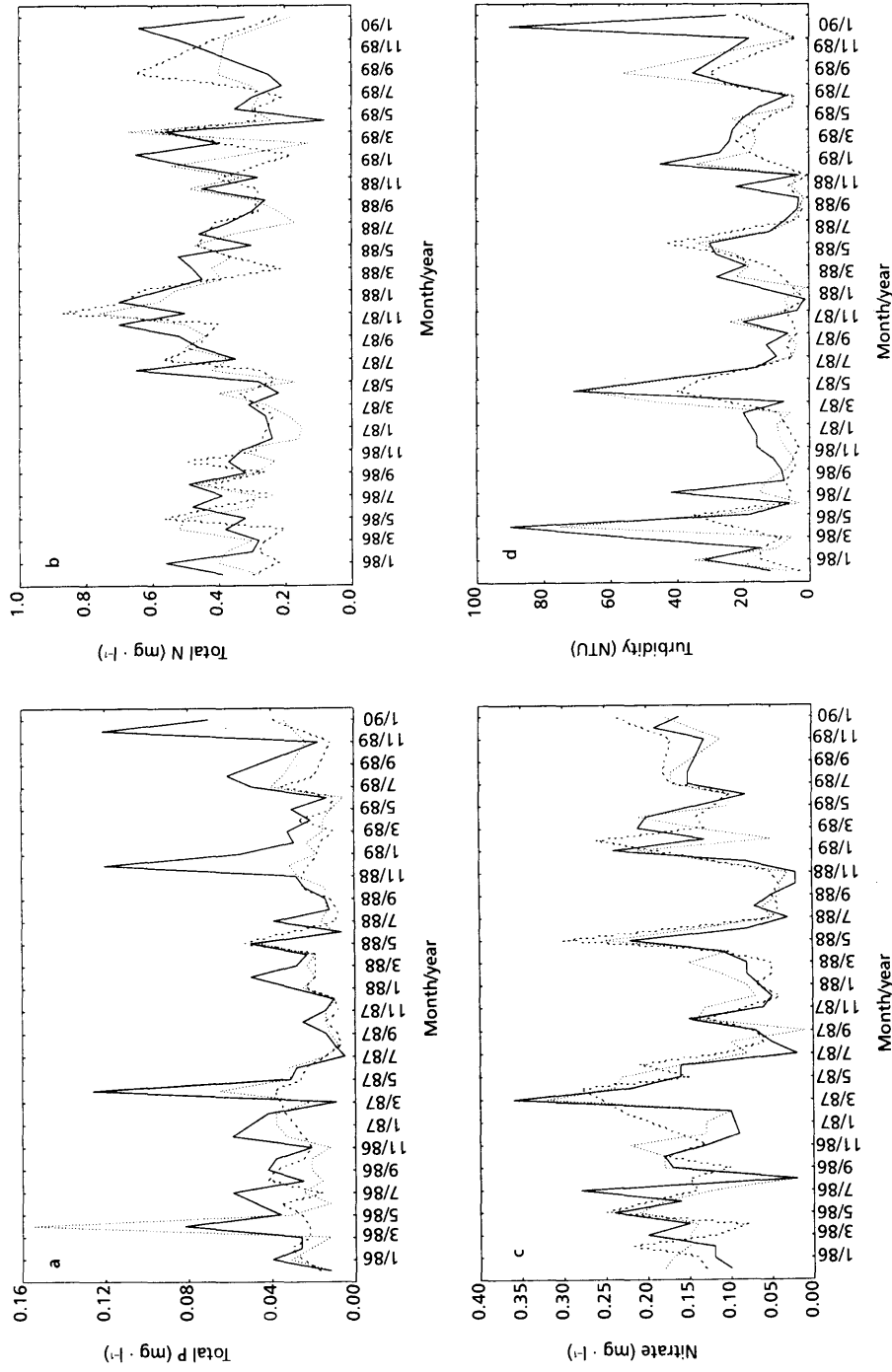
The temporal variation in total phosphorus in Itaipu Reservoir (Figure 3a) can be considered as stationary. In other words, the serial dependency among observations is only a function of their distance and the mean total phosphorus concentration in each zone. For the time interval analyzed ( $N = 4$  years) it showed a fixed mean. An important implication of this result is the absence of eutrophication in Itaipu Reservoir. This constancy in phosphorus concentration could be due to the fact that a major part of the load is retained in upstream reservoirs, in the basins of the rivers Grande, Tietê, and Paranapanema. The nutrient retention in upstream reservoirs has long been considered the main process, which inhibits the acceleration of eutrophication in reservoirs lower in the Upper Paraná River (Tundisi *et al.*, 1993). Therefore, the main sources of phosphorus loads in Itaipu Reservoir are limited to tributaries, and the floodplain upstream (Agostinho *et al.*, 1995); however, most of this phosphorus is retained in the upper third of the reservoir through sedimentation (FUEM/NUPELIA/ITAIPU BINACIONAL, 1998). Alternatively, this apparent lack of eutrophication may reflect our inability to detect small changes within a four-year time series. Total nitrogen, nitrate, and turbidity did not exhibit obvious seasonal patterns (Figure 3).



**Figure 2** Time series (a) and autocorrelation function (b) for dissolved oxygen in Itaipu Reservoir.

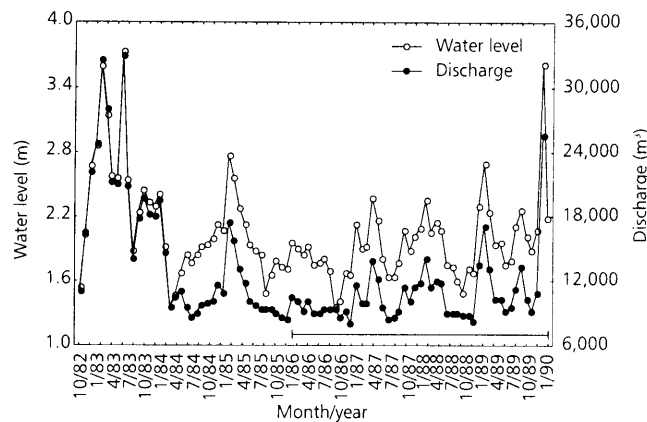
Limnological variables were strongly correlated among the riverine, transition, and lacustrine zones of Itaipu Reservoir. This correlation suggests that a major part of the non-seasonal variability could be accounted for by hydrodynamic processes, specifically discharges by the Paraná River (Figure 4). The irregularities of discharges from the Paraná River, partially regulated by dams upstream (Agostinho *et al.*, 1992), determine irregularities in the dynamics of the limnological variables.

Analyses of time series with intervention are being conducted to quantify the influence of the discharge on the dynamics of limnological variables in Itaipu Reservoir (Bini *et al.*, in prep).



**Figure 3** Time series for total phosphorus (a), total nitrogen (b), nitrate (c) and turbidity (d) in Itaipu Reservoir.

Thus, other than seasonal trends, no long-term trends could be identified with the data available for Itaipu Reservoir. We suspect that after the original upsurge, changes in the abiotic environment decelerated. The presence of a more constant environment with reservoir aging probably leads to less fluctuation in species composition and high biotic stability. Nevertheless Itaipu Reservoir is the last one in a cascade of reservoirs in Upper Paraná River, and thus suffers less eutrophication. We suspect more pronounced alterations occur in other reservoirs in the basin, because of the input of untreated effluents from domestic and industrial sources and from agricultural runoff (Tundisi *et al.*, 1993). Time series longer than the ones available are necessary to describe such trends.



**Figure 4** Discharge and water level time series for the Paraná River just above Itaipu Reservoir. The horizontal line indicates the interval for which the limnological data were available.

#### *Aquatic Macrophytes*

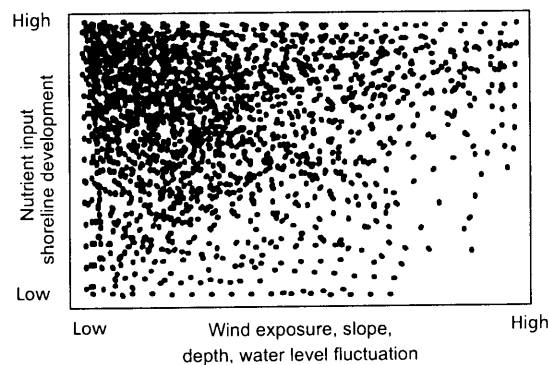
The formation of a reservoir strongly influences the conditions that determine diversity and abundance of aquatic macrophytes. Inundation of terrestrial areas could be beneficial to the development of aquatic macrophytes, if there is an increase in spatial heterogeneity. For instance, a river that runs through a canyon may expand into the riparian zone once the basin is flooded, enhancing habitat suitability. But, when the inundated terrestrial habitat has a high habitat diversity (e.g., wetlands, lagoons), simplification of the environment by impoundment can lead to a reduction of diversity and area available for colonization (Thomaz & Bini, 1998a).

Other factors associated with the formation of a reservoir that affect aquatic macrophytes abundance and species diversity include i) reduction in water velocity to develop areas adequate for attachment; ii) increases in sedimentation to increase nutrient concentration in the water and sediments, and decrease light penetration; iii) alterations in hydrological regime; and iv) an increase in nutrient cycling (Thomaz & Bini, 1998a).

Independently of immediate or intermediate term effects, the formation of reservoirs entail the creation of lentic environments that will necessarily show an ecological succession characteristic of lacustrine environments. In other words, sooner or later, natural or artificial eutrophication and reduction in depth will lead to the development of various species of aquatic macrophytes (Thomaz & Bini, 1998b).

In general, the degree of aquatic macrophytes development for a given reservoir is associated with factors such as depth, slope, shoreline development ratio, degree of wind exposure, nutrient inputs, and water level fluctuation (Thomaz & Bini, 1998b). These characteristics predict, with certain limits, the intensity of development of aquatic macrophytes after impoundment.

Hypothetically, development of macrophytes will be best in shallower reservoirs, with relatively constant water levels, high nutrient inputs, and higher values of the shoreline development ratio (Figure 5).



**Figure 5** Hypothetical tendency of colonization of aquatic macrophytes in reservoirs. The degree of colonization is directly related with points density (after Thomaz and Bini, 1998b).

There have been several studies about the effect of impoundment on the mid- to long-term dynamics of aquatic macrophyte communities in temperate regions (Krahulec & Kaplan, 1994; Rorslett & Johansen, 1996; Królikowska, 1997), but there is a lack of information for tropical and neotropical regions. Massive development of free-floating macrophytes have been observed in the first stages of many tropical reservoirs such as Tucuruí, Amazon River Basin (Tundisi, 1994), and Kariba, Africa (Mitchell *et al.*, 1990). Such extensive development of aquatic macrophytes depends on conditions such as absence of strong winds, low water turbulence, and availability of propagules or other sources of dispersion, all of which must occur simultaneously with nutrient increases typical of filling phases (Esteves & Camargo, 1986; Thomaz & Bini, 1998a). These conditions favor free-floating species particularly *Eichhornia crassipes*, *Pistia stratiotes* and *Salvinia auriculata* whose populations can experience tremendous increases during and soon after filling, constituting potential threats to multiple uses of reservoirs.

Results from studies at Itaipu Reservoir indicate that impoundment produced a favorable environment for development of aquatic macrophytes and their species diversity. Itaipu Reservoir is a typical example of a canyon being transformed into a lake, resulting in the development of suitable habitats for aquatic flora. Before impoundment, 24 species were identified in tributaries within the reservoir basin (SUREHMA, 1980), whereas 62 were recorded 15 years after impoundment (Thomaz *et al.*, 1998). The most important factor related to increased species diversity in this reservoir is perhaps the moderate water level fluctuations (< 1.0 m). In contrast to the absence or excessive water level fluctuation, moderate fluctuations generate increased habitat diversity (Rørslett, 1991; Rørslett & Johansen, 1996). However, observed responses should be viewed with caution because the pre-impoundment survey was limited to tributaries and excluded other aquatic habitats within the basin.

An interesting development has been the extensive colonization of Itaipu Reservoir by submersed macrophytes, relative to natural ecosystems in the basin. Five submersed macrophytes species have been identified in the floodplain of the Middle Paraná River in Argentina (Neiff, 1986), six in the floodplain of the Upper Paraná River in Brazil (S.M. Thomaz, unpublished data), and 14 in Itaipu Reservoir (Thomaz *et al.*, 1998). Other than limited water level fluctuations, reduced water velocity and increased light penetration contribute to the high development of submersed macrophytes in embayments of Itaipu Reservoir.

*Egeria najas*, a submersed Hydrocharitaceae, is the most extensively distributed macrophyte in Itaipu Reservoir. Expansion within some embayments in the eastern side of the reservoir appeared to be random, and sampling revealed presence of *E. najas* in 16 to 54% of the sites sampled within each arm, with biomass ranging from 28 to 234 gDW m<sup>-2</sup> (Thomaz *et al.*, 1998; Thomaz & Bini, 1998a). This species was not detected during pre-impoundment surveys (SUREHMA, 1980), and it is considered rare in the floodplain of the Paraná River in Argentina (J. J. Neif, personal communication), and the floodplain of the Upper Paraná River (S. M. Thomaz, unpublished data).

For reservoir chains, position in the series is also an indicator of potential for macrophyte colonization. The creation of suitable environment for development of submerged macrophytes seems to be a characteristic of reservoirs located at the end of the cascade. Reservoirs in this position receive water with reduced suspended loads, and consequently, light penetration in the water column is high. This observation is corroborated by the excessive development of *Egeria* in Paulo Afonso (São Francisco River) and Jupia (Upper Paraná River) reservoirs, both located at or near the end of reservoir cascades. The excessive development of macrophytes (specially *Egeria*) is negatively affecting hydropower generation in both of those reservoirs (ITAIPU BINACIONAL, 1997).

### *The Fish Fauna*

The events that follow impoundment are determined by the environmental conditions that exist during critical periods, such as filling and beginning of the dam operation. In those reservoirs where the anoxia is localized, there are major alterations in the community structure, with drastic changes in species abundance or even local extinctions. Alternatively, in those reservoirs where anoxia extends to most of the reservoir,



the colonization process is began after the aerobic conditions are reestablished, by fish that have remained in the periphery of the reservoir. In the Paraná River Basin, where the human population density is high and has cleared much of the forests in the last 50 years to develop agriculture, the inundated plant biomass is often less than in the Amazon River Basin, resulting in less severe oxygen depletions. However, impoundment of agricultural basins can inundate areas where chemical fertilizers, pesticides, and herbicides have been applied intensively, also contributing to poor water quality during and immediately after filling (Tundisi *et al.*, 1993).

The high biological production in the first few years after the impoundment is a result of an enormous liberation of dissolved nutrients by the submersed organic matter during decomposition (see previous sections). In general, nutrient surges cause an increase in production at all trophic levels (O'Brien, 1990). This stage of high production has been termed trophic upsurge period (Kimmel & Groeger, 1986), and its duration varies. As physical, chemical, and biological processes tend to be faster in tropical latitudes, the trophic upsurge is expected to be shorter in neotropical than in temperate reservoirs (Williams *et al.*, 1998).

Eventually, there is a reduction in nutrients through processes such as sedimentation and exports via discharges, and in fish production through reduction of nutrients and depletion of the original populations via natural mortality or human exploitation. The new rate of production should be in between that of the original river and a natural lake (Balon, 1974; Noble, 1986; Randall *et al.*, 1995; Williams *et al.*, 1998). The tendency towards trophic depletion that characterizes the majority of reservoirs few years after formation (Ribeiro *et al.*, 1995), may be reverted through drawdowns that produce prolonged periods of low water level. This allows aeration of bottom sediments and development of vegetation in the regulated zone. Refilling of the reservoir simulates, at a smaller scale, the processes linked to the filling stage described above. Water level manipulation to increase fish recruitment and biogenic capacity of reservoirs has been reported by several authors (e.g., Bennett, 1970; Noble, 1980; Martin *et al.*, 1981; Mitzner, 1981; Rainwater & Houser, 1982; Beam, 1983; Miranda *et al.*, 1984; Ploskey, 1985; Summerfelt, 1993; Hayes *et al.*, 1993). In Sobradinho Reservoir (São Francisco River Basin) this process has been associated with extraordinary variations in yield of the artisanal fishery (Agostinho, 1998). The trophic depletion can be delayed by input of nutrients from anthropogenic activities.

In the next five subsections we turn our attention to the temporal patterns associated with colonization of reservoirs by fish after the initial filling stage. Although we focus on temporal patterns, temporal effects are sometimes analyzed according to spatial zones. We begin by considering reproductive efforts during colonization, because this topic is critical to interpreting observations about species diversity and abundance, also considered in this section. Lastly, we examine information on fish size and trophic structures.

### **Variations in Reproductive Effort**

Reproductive strategies are generally more conservative than other vital activities, imposing biogenic limitations to colonized reservoirs. The most obvious limitation of

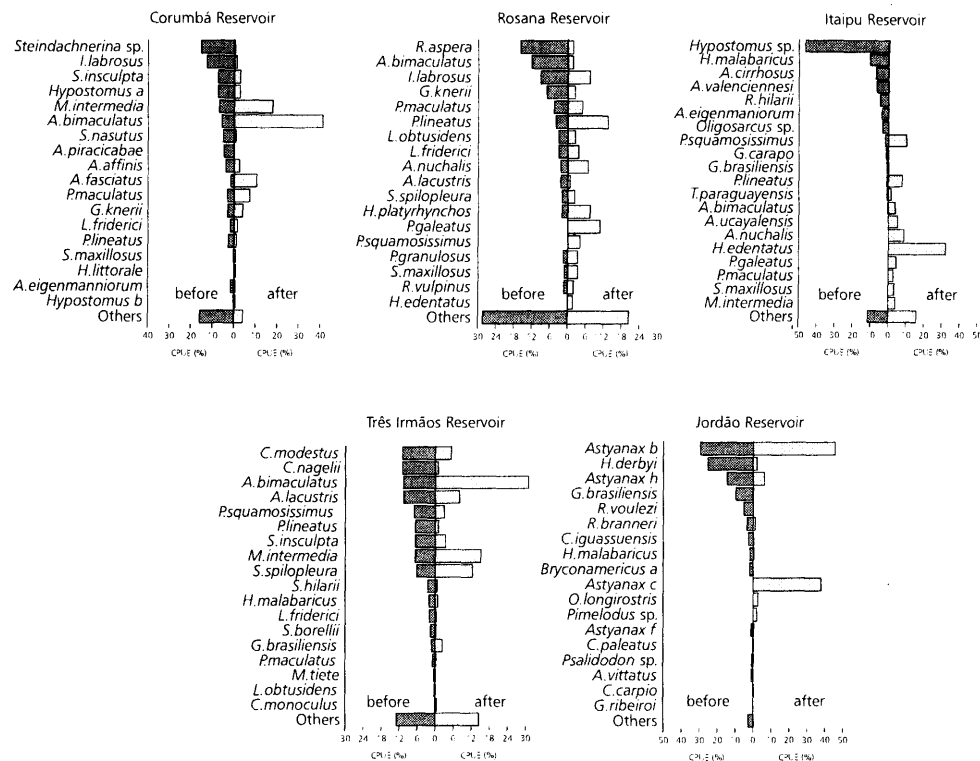
impoundment is the restriction or elimination of access to long fluvial stretches. The combined effect of a series of dams in the main tributaries of the Upper Paraná River has been the virtual absence of large migrators (Lowe-McConnell, 1987). Conversely, long unimpounded stretches above reservoirs have been linked to the presence of migratory species in some reservoirs of the Upper Paraná River Basin (Agostinho, 1994). Alteration of hydrodynamics could impose restrictions on reproductive output of the local fauna by changing conditions of dissolved oxygen, temperature, and flow velocity to unfavorable levels. Open areas with low turbidity can increase predation on eggs and larvae. Short-term water level fluctuations caused by operation of the dam reduce reproductive success, especially when adhesive or nest-reared eggs are released near the shore, potentially influencing recruitment of many fish species in a reservoir (Suzuki & Agostinho, 1997). Lastly, suitable spawning habitats for the original fish fauna (e.g., rocks, gravel, and sand) may become inaccessible by excessive depth.

Fish exhibit enormous variability in reproductive strategies (Wootton, 1990). Reproductive strategies include adaptations such as age at maturation, fecundity, size and type of gametes, spawning period and habitat, reproductive behavior, type of oocyte development, and sex ratio. These strategies often adjust to the environmental conditions encountered, and represent a homeostatic response to minimize energetic costs. According to Dias (1989), the most flexible reproductive strategies are time of spawning and, possibly, spawning habitat. Size at maturation is also flexible, within species-specific limits. Other strategies like parental care and type of gametes (e.g., adhesive, buoyant) are more inflexible.

In reservoirs, it is expected that species with higher plasticity in spawning habitat should be among the most successful colonizers. However, it has been verified that to reproduce, most species that colonize neotropical reservoirs search for lateral tributaries, upstream stretches, or other lotic areas (Agostinho *et al.*, 1995; Suzuki & Agostinho, 1997; Vazzoler *et al.*, 1997). In Itaipu Reservoir, six of the ten principal species in the commercial fishery use the upstream floodplain for spawning and nurturing (Agostinho *et al.*, 1994a). Have relations between reproductive strategies and colonization success been documented in neotropical reservoirs? Analyses of fish communities that developed in some of the reservoirs in the Paraná River Basin offer some evidence (Figure 6). Time of year when the dam is closed and time needed to fill the reservoir interact with time of migration and time of spawning to influence the type of community that develops in the reservoir shortly after impoundment.

The formation of Corumbá Reservoir, impounded in September 1997, overlapped with the reproductive period of many species. The most successful spawners were those that produce small eggs and hatched promptly, and included *Astyanax bimaculatus*, *A. fasciatus*, *Moenkhausia intermedia*, *Pimelodus maculatus*, *Galeocharax knerii*, and *Leporinus friderici*. The first three species began recruiting to the experimental fishery three months after filling. All these species have eggs that mature at less than 1.1 mm diameter, high fecundity, short embryogenesis, and short hatching times. Lamas (1993) reported that embryogenesis time for 52 freshwater fish species ranged from 330 to 5,365 degree-hours (sum of the water temperature each hour, in Celsius degree), with *A. bimaculatus* and *P. maculatus* having some of the lowest values (446 and 400, respectively). Nevertheless, among the species whose abundance decreased, some had favorable egg

characteristics, although this differed in feeding habits (illiophages and benthophages; Fuem-Nupelia-Furnas, 1998) or were typically rheophilic (Agostinho & Julio Jr., 1994).



**Figure 6** Proportion of the main species (number of individuals per 1,000 m<sup>2</sup> gill net 24 h<sup>-1</sup>) before and two years after impoundment of five reservoirs in Paraná River Basin.

Also, when comparing congeneric species (e.g., *Steindachnerina* sp. versus *S. insculpta* and *Apareiodon piracicabae* versus *A. affinis*), the most successful congener was usually the one whose eggs were the least adhesive and had the thinnest radiate zone (Suzuki, 1992). Species that produce large, adhesive eggs are expected to find development restrictions in environments where water level is variable and where dissolved oxygen is low near the bottom. Moreover, large eggs are characteristic of species that provide parental care and exhibit territorial behavior (Suzuki, 1999). This strategy is often inadequate in environments with periodic water level fluctuations.

Proliferation of small characids, especially tetragonopterins, has been documented, after impoundment, in several reservoirs (Figure 6). At Três Irmãos Reservoir *A. bimaculatus* was dominant and had an omnivorous diet with tendency to insectivory. In Corumbá Reservoir, this species was also dominant but had a herbivorous diet. In Jordão Reservoir (Iguaçu River) *Astyanax* (undescribed) was dominant and herbivorous, whereas *Astyanax c* was the second most abundant species and detritivorous. In Segredo Reservoir

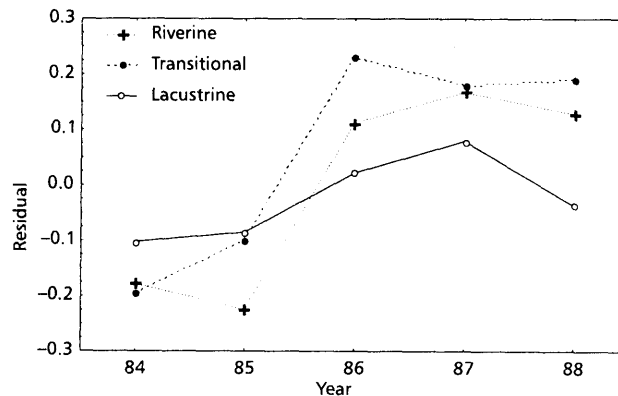
(Iguaçu River) the dominant species were the same as in Jordão Reservoir (Hahn *et al.*, 1997). In Rosana and Itaipu reservoirs, these species were replaced by *A. nuchalis* and *Parauchenipterus galeatus*. These two species have internal fertilization. *Agenciosus ucayalensis* and *A. valenciennesi* had reproductive strategies similar to *Auchenipterus nuchalis* and *P. galeatus*, and were among the ten most important species two years after impoundment of Itaipu Reservoir. Conceivably, internal fertilization may be advantageous in the first years of impoundment (Agostinho *et al.*, 1994a).

*H. edentatus* (zooplankton filter-feeder) proliferated very fast in Itaipu Reservoir, colonizing the pelagic zones of the reservoir. One characteristic that gives this species an advantage is its large number of small eggs (0.75 mm diameter) spawned in several batches (Suzuki, 1992), pelagic eggs and larvae (Nakatani *et al.*, 1998), and capability of spawning in two widely separate periods of the same year (Benedito-Cecilio *et al.*, 1997). A different pattern was obtained in two temperate reservoirs where the development of planktivorous fish population reaches its peak several years after damming (Straškraba *et al.*, 1990). *H. edentatus* is also present in Rosana Reservoir, but its abundance is low, perhaps because few were trapped when the dam was closed. In Rosana Reservoir, the most abundant species in the experimental fishery was the migratory *Prochilodus lineatus*. Juveniles occurred in high densities floodplain lagoons, and adults concentrated in the pre-impoundment basin because Capivara Dam prevented further upstream migration.

To evaluate fluctuations in reproductive effort (*sensu* Miller, 1984) during the formative years of Itaipu Reservoir, we examined fluctuations in the gonadal weights of mature fish during the first 5 years after impoundment. To exclude possible effects of fish size, the analysis was based on residuals of a linear regression between gonad weight and fish weight (Figure 7). Statistical analyses showed a lower reproductive effort in the first two years (1984-1985), with increases thereafter. Reproductive effort differed among zones, but there were statistical interactions between time and zone. The interactions indicated that temporal changes in gonad weight were not the same in all zones, being less pronounced in the lacustrine zone.

Species with small eggs and simple reproductive strategies seem to thrive in new reservoirs, whereas species with more elaborate reproductive strategies such as intricate courtship, nest construction, and parental care begin to make gains as reservoirs mature. In the Paraná River, species with parental care contributed little to the composition of the fish community (0%-8% by number) in new reservoirs including Rosana, Segredo, and Três Irmãos, but their contribution increased (15%-24% by number) in reservoirs age 15 years or older including Promissão, Ibatinga, and Itaipu (Suzuki, 1992; CESP, 1996; Agostinho *et al.*, 1997a; FUEM/NUPELIA/ITAIPU BINACIONAL, 1998). The participation of species with parental care in the community appears to be even higher in old and shallow reservoirs (up to 40%; FUEM/NUPELIA/COPEL, 1998a). Proliferation of aquatic macrophytes, that may require many years, seems to promote abundance of species with elaborate reproductive strategies. In Itaipu Reservoir, increased abundance of *Hoplias malabaricus* (Erithrinidae) and cichlid species coincided with the development of aquatic macrophyte communities in some arms of the reservoir.

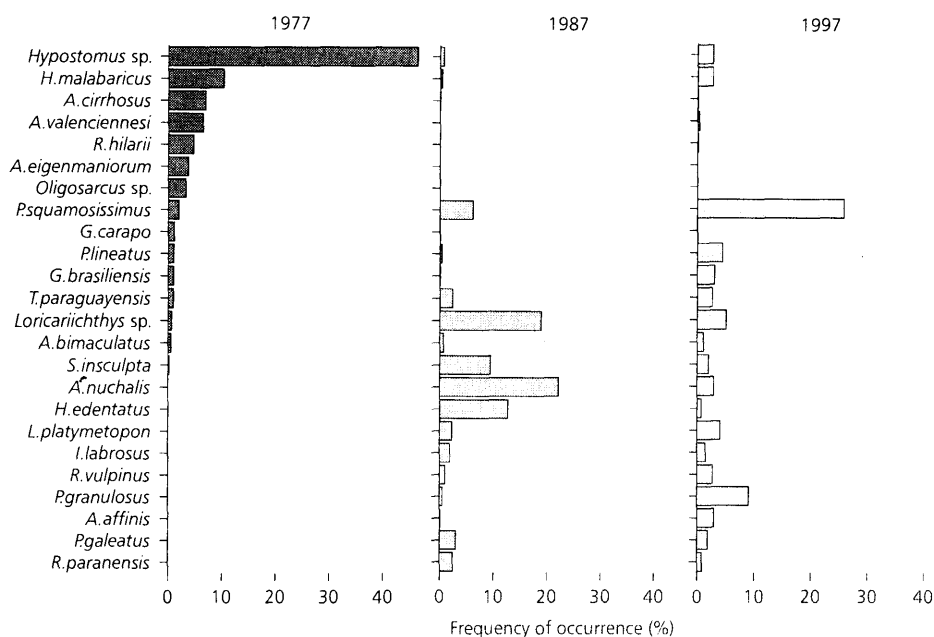
An analysis of the differences in abundance of the main species before impoundment (1977), 5 years after (1987), and 15 years after impoundment (1997) suggested that the fish community may have reached some level of stability (Figure 8). Bray-Curtis distance analysis (Krebs, 1989) indicated high dissimilarity between before impoundment and 5 years after ( $B = 0.80$ ), lower dissimilarity between before impoundment and 15 years after ( $B = 0.68$ ), and even lower dissimilarity between the 1987 and the 1997 post-impoundment communities ( $B = 0.37$ ). These results suggest that the community changed less after 1987 than between pre-impoundment and 1987 or 1997. The lower dissimilarity between pre-impoundment and 15 years after, than between pre-impoundment and 5 years after, suggests that some elements of the local fauna entered or proliferated in the reservoir after the fifth year of impoundment.



**Figure 7** Changes in weight of fish gonads during the first 5 years after impoundment of Itaipu Reservoir, according to longitudinal zones. The variable analyzed was the residuals derived from a linear regression between the gonad weight and fish total weight (both log-transformed).

Out of 31 species for which we have detected reproductive activity in Itaipu Reservoir, 11 showed the first evidence in 1986, 4 years after impoundment. Eight of these species, including *P. squamosissimus*, *Steindacnerina insculpta*, *Catathyridium jenynsii*, *Loricariichthys* sp., *L. platymetopon*, *Loricaria* sp., *S. marginatus*, and *Porotergus ellisi* reproduce in the reservoir. Except for *P. squamosissimus*, abundant since impoundment, adults of these species were collected only sporadically in the first 3 years. Spawning areas of *P. squamosissimus* in 1986 were lotic stretches of lateral tributaries, where this species occurred only during the reproductive period. After 15 years, the areas used by *P. squamosissimus* for spawning have been notably expanded to include lentic parts of the tributaries and littoral areas of the reservoir (FUEM/NUPELIA/ITAIPU BINACIONAL, 1998). The success of this species in colonizing Itaipu and other reservoirs in the Paraná River Basin may be attributed to its reproductive strategy. *P. squamosissimus* produces small (0.5 mm diameter), pelagic (Fontanele & Peixoto, 1978), buoyant eggs spawned in several batches during the reproductive period. Larvae are also pelagic (Nakatani *et al.*, 1993). Three

other species essentially reproduce in the riverine zone of Itaipu Reservoir including *A. nuchalis*, *A. ucayalensis*, and *Iheringichthys labrosus*.



**Figure 8** Frequency of occurrence (%) of the main species collected in Itaipu Reservoir in 1977, 1987, and 1997. The reservoir was impounded in 1982.

We could not detect reproduction in 18 out of over 60 species in the experimental fishery. Among them are long-distance migrators such as *Salminus maxillosus*, *Pseudoplatystoma corruscans*, *P. maculatus*, *P. lineatus*, *Paulicea luetkeni*, *Pinirampus pirinampu*, *Leporinus elongatus*, *L. obtusidens*, *Hemisorubim platyrhynchos*, *P. granulatus*, *Rhinelepis aspera*, and *R. vulpinus*. Other species for which reproduction was not detected include *A. valenciennesi*, *S. altoparanae*, *S. borellii*, *Sorubim lima*, *Cyphocharax modestus*, and *C. nagelli*. These species are not considered long-distance migrators (Vazzoler, 1996), but may require short migrations into lotic environments to spawn.

*H. edentatus*, a pelagic and planktophagous species that produces many small eggs, laid in several batches, inside Itaipu Reservoir, seemed to be destined to successful occupation of the reservoir. After the first few years, this species was one of the most abundant in the commercial and experimental fishery (Agostinho *et al.*, 1994a, b). But catches dropped sharply in recent years. This reduction may be linked to the end of the trophic upsurge. Alternatively increased predation pressure by increased abundance of *P. squamosissimus*, who prey on juveniles of *H. edentatus* (Agostinho & Julio, 1996), and overfishing (Agostinho *et al.*, in press), are possible. The concurrent decrease of *H. edentatus* and *A. nuchalis* whose juveniles have a similar diet, but *A. nuchalis* does not provide a substantial fishery and their juveniles are not preyed on by *P. squamosissimus*, suggests that decreases in abundance of *H. edentatus* could be associated with reductions in food

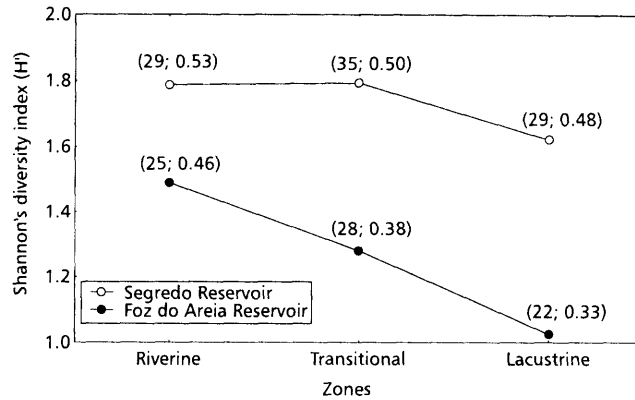
availability. Unfortunately, no data on zooplankton densities are available for the period of concern.

### Diversity of the Fauna

The years needed by a fish community to reach temporal stability after impoundment ranges from several to many. Lowe-McConnell (1987) reports periods of 6 to 10 years for Russian reservoirs at latitudes up to 55°N, and from 25 to 30 years in reservoirs at higher latitudes. In temperate reservoirs in North America, instability has been associated with the first 5-10 years after impoundment (Ploskey, 1981; Benson, 1982; Adams *et al.*, 1983). Balon (1974) concluded that Kariba Reservoir (Zambezi River, Africa) reached stability by about the tenth year after impoundment. Other than latitude, composition of the pre-impoundment fauna, size of the drainage basin, water retention time, length of the stretch without dams upstream, presence of large lateral tributaries, and design and operation of the dam are factors that can influence time to stability. Large, non-cyclic perturbations related to operation of the dam contribute to instability of the community structure, and reduction of species diversity and stock sizes. Such reductions are evident in the oldest (23 years) reservoir in the Paraná River Basin (Agostinho *et al.*, 1997b). Thus, large and random fluctuations in water level can slow down stabilization of reservoir fish communities, and lead to oscillations in the population of r-strategists (short longevity, high reproductive capacity) species, and denter seasonal and k-strategists (*sensu* Winemiller, 1989) that typify the largest neotropical fish species. Nevertheless, as identified earlier, water level manipulations can be used as a management strategy that simulates flood events and generate instability beneficial to fish communities.

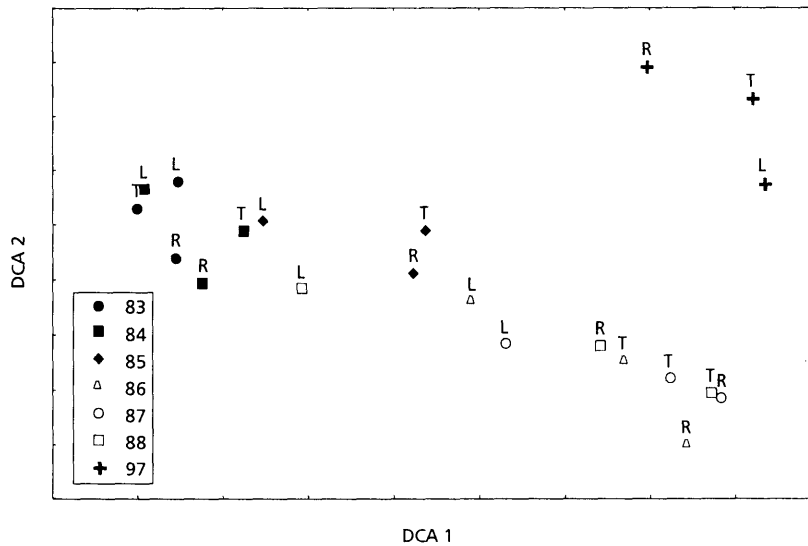
Segredo and Foz do Areia reservoirs are contiguous in the Iguaçu River, with the inundated area of the former reaching the dam of the latter. Conceivably, both reservoirs should have inherited the same species assemblages from the river, and thus both reservoirs would be expected to have a similar species assemblage. However, it is conceivable that the presence and operation of Foz do Areia Dam upstream, including stoppage of water releases during filling of Foz do Areia, may have handicapped the fish assemblage that eventually developed in Segredo Reservoir. Surveys conducted when Segredo and Foz do Areia were 1 and 14 years old, respectively, indicated statistically lower species diversity, evenness, and Shannon diversity in the older reservoir (Figure 9). Also, reductions proved to be increasingly pronounced as the reservoir transition from the riverine to the lacustrine zone. We suspect that loss of diversity in Foz do Areia Reservoir is an effect of aging.

Patterns of  $\beta$  diversity in Itaipu Reservoir according to years and zones were analyzed by Detrended Correspondence Analysis (DCA).  $\beta$  diversity is a measure of how different (or similar) a set of samples are in relation to species composition and abundance. The fewer species that are shared, the higher the  $\beta$  diversity (Magurran, 1988). For the two first axes, annual variance was substantially greater than variance among reservoir zones, suggesting that the pattern of  $\beta$  diversity for Itaipu Reservoir varied principally along years (Figure 10). Also, DCA suggested that the differences among the lacustrine, transition and riverine zones tended to increase temporally (exception was 1997, when the similarity among the zones increased). We conclude that in a large reservoir with distinct habitats such as Itaipu, there is a temporal increase in  $\beta$  diversity with time, and thus a reduction in the number of species that are shared among the habitats considered.



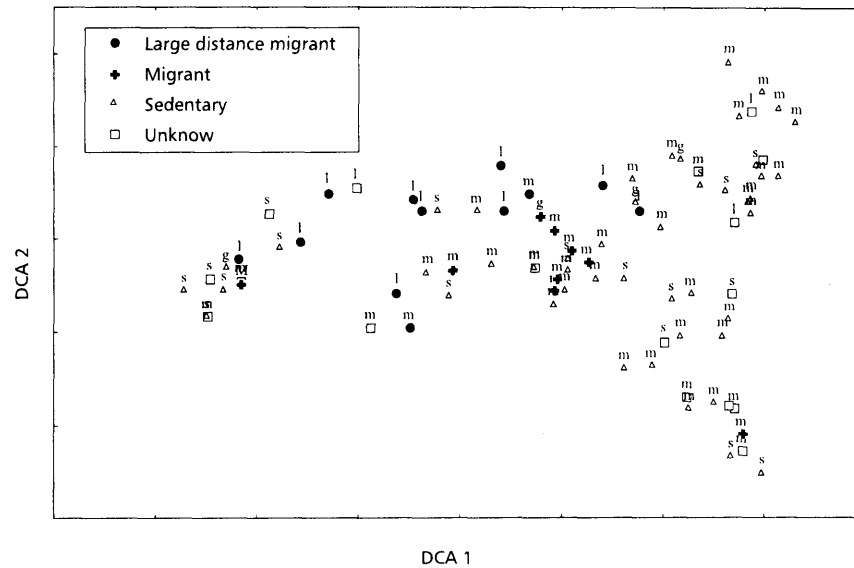
**Figure 9** Values of Shannon's diversity index for the fish community in Segredo Reservoir (at age 1) and Foz do Areia Reservoir (at age 14), according to zones. Numbers in parentheses indicate species diversity and evenness, respectively.

Examination of species dispersion using DCA axes 1 and 2 indicated that long-distance migrators and large-bodied (SL > 50 cm) fish were at their peak abundance shortly after impoundment (i.e., concentration of l's in Figure 11 coincide with position of initial years in Figure 10). Contrastingly, in recent years the fish assemblage has been dominated by sedentary and medium-sized (SL = 20–50 cm) species (i.e., concentrations of s and m's in Figure 11 coincide with position of recent years in Figure 10).



**Figure 10** Scores of zones and years derived from a DCA of Itaipu Reservoir (R = riverine; T = transitional; and L = lacustrine; 83-97 indicates sampling years).





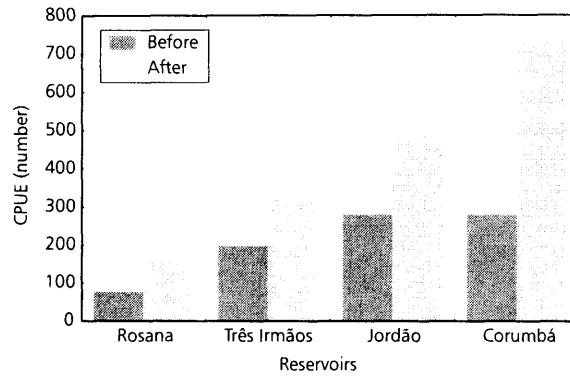
**Figure 11** Scores for species classified by size and migratory behavior derived from a DCA of Itaipu Reservoir (S = small-sized species, SL < 20 cm; M = medium-sized species, SL = 20-50 cm; L = large-sized species, LS > 50 cm).

### Variations in Abundance

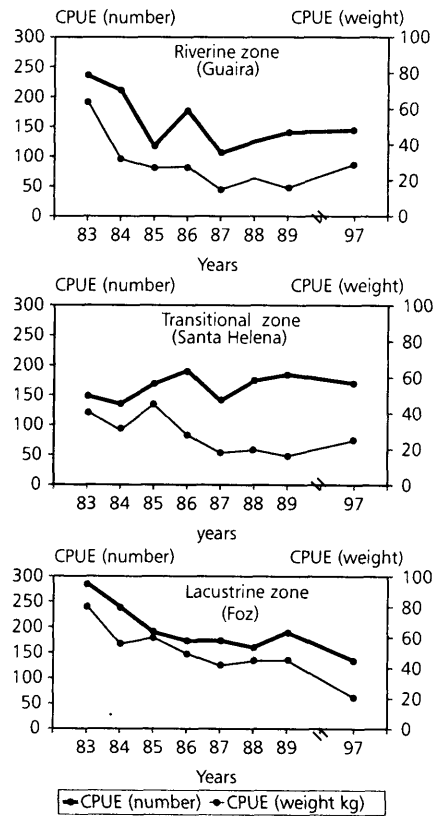
Fish abundance and species diversity change following impoundment. Statistical comparisons of before-and-after catch per effort data in four impoundments revealed an increase in fish abundance after impoundment (Figure 12). In Itaipu Reservoir, catch per effort after the impoundment (1983-1997) revealed distinct tendencies depending on the longitudinal zone considered (Figure 13).

In the riverine zone there was a sharp decrease in catch per effort just after impoundment, followed by large oscillations. In the transitional zone, catches in number oscillated near the values recorded just after impoundment, but catches in weight exhibited a decreasing trend after the third year of impoundment, suggesting a transition towards smaller individuals. In the lacustrine zone there was a decreasing trend in catches by number and weight after impoundment.

A multiple regression analysis on the source of variability in catch per effort among reservoirs revealed that reservoir area (8-1,350 km<sup>2</sup>), age (1-23 years), and water residence time (1-118 days) accounted for most of the variability ( $R^2 = 0.88$ ). This analysis postulated that fish abundance decreased with age and area, and increased with residence time. However, data from only nine reservoirs (Itaipu, Segredo, Areia, Corumbá, Rosana, Três Irmãos, Promissão, Ibitinga, and Nova Avanhandava) were available for analysis. Thus, this result should be considered as preliminary.



**Figure 12** Catch per effort (individuals per 1,000 m<sup>2</sup> gill net 24h<sup>-1</sup>) before and after two years of damming of four reservoirs in the Paraná River.

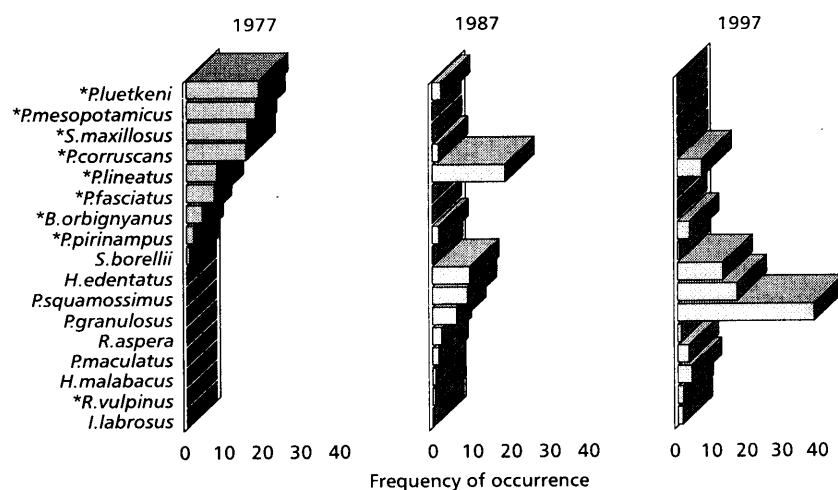


**Figure 13** Variations in the catches per 1,000 m<sup>2</sup> gill net 24 h<sup>-1</sup> (number of individuals and weight, kg) in the experimental fishery at Itaipu Reservoir. Note the broken x-axes. Names in parentheses identify the localities near which samples were collected. Dam was closed in October 1982.

### Variations in Size

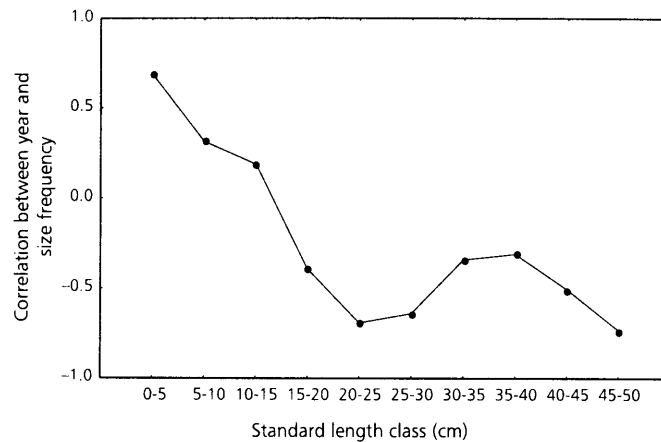
One of the most notable impacts of impoundment is a reduction in the average body size of the species that constitute the fish community of a reservoir. Such reductions have been documented by several authors (Araujo-Lima *et al.*, 1995; Agostinho *et al.*, 1995; Petrere, 1996; Benedito-Cecílio *et al.*, 1997), and have an important effect on the fisheries. The virtual disappearance of large-bodied species, often piscivorous migrators, not only influence yield, but also fishing methods, fish marketing, and commercial value (Agostinho *et al.*, in press).

Large migratory species were among the eight most important species in the fishery of the Itaipu basin prior to impoundment (Figure 14). Six of them reached sizes over 1 m and six were exclusively piscivores. Some of these species are still occasionally caught in the reservoir and adjacent tributaries, but command commercial values ranging 2-4 times higher than the highest value of the fish commercialized nowadays in the Itaipu Reservoir fishery (Agostinho *et al.*, 1994b).



**Figure 14** Fish species composition in the landings of the commercial fishery in Itaipu Reservoir, before (1977), and after impoundment (1987 and 1997). Species names in bold are long-distance migrators; an asterisk identifies the species reach lengths over 60 cm (after Agostinho *et al.*, in press).

Analysis of the experimental fishery data corroborates the tendency for a gradual reduction in fish sizes over time. A Pearson correlation analysis between fish abundance and age of Itaipu Reservoir between 1983 and 1997, according to length groups, revealed that the frequency of small-bodied fish is positively correlated with time. Abundance of the most frequent sizes in this time period (15-30 cm), and the larger ones (40-50 cm), were negatively correlated with time (Figure 15).



**Figure 15** Pearson correlation coefficients between fish abundance and age of Itaipu Reservoir between 1983 and 1997, according to length groups.

### Variations in Trophic Structure

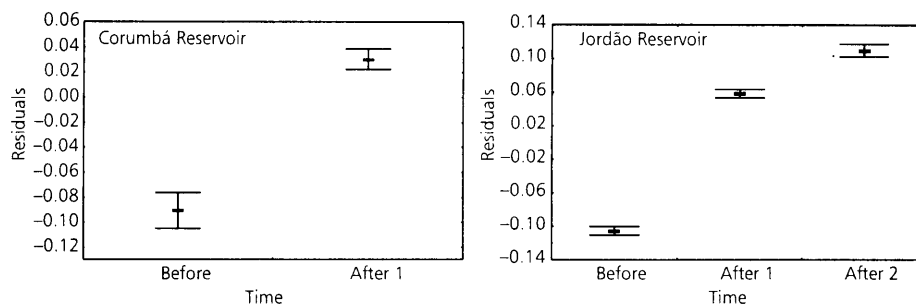
The incorporation of terrestrial organic matter into the aquatic system during the filling stage and immediately after impoundment produces staggering increases in food availability, specially for small-bodied fish species that are often insectivores, herbivores, or omnivores. Such increases in abundance of small-bodied fish usually also lead to an increase in abundance of piscivores. High nutrient loads and high biological production assure high productivity for a longer period, especially for planktivorous fish (Tundisi *et al.*, 1993).

Also, there is an enhanced availability of substrate elicited by the flooding of terrestrial vegetation and other structures, which are colonized by periphyton. This periphyton is available to illiophagous fish (Petriere, 1996; Agostinho & Gomes, 1998). In the fishery at Itaipu Reservoir, a decreasing trend in yield of illiophagous species has been attributed to the loss of flooded terrestrial vegetation (Agostinho *et al.*, 1993b; Gomes & Agostinho, 1997). As the terrestrial vegetation disintegrates, nutrient releases and availability of attachment substrate wanes, contributing to a decrease in overall productivity.

The copious food supply available just after impoundment produced a substantial increase in consumption relative to the pre-impoundment period. A comparison of the relation between stomach weight and body weight in Corumbá and Jordão reservoirs using residual analyses, indicated that stomach weight increased substantially after impoundment (Figure 16), and suggested high feeding intensity.

We analyzed the percentage contribution of trophic groups to the colonization of Corumbá, Jordão, Três Irmãos, Rosana, Itaipu, and Tucuruí reservoirs. Data collected the year before and two years after impoundment did not allow definition of a unique colonization pattern by each of the trophic groups, except for the reduction in abundance of detritivores-illiophages that are the dominant group in all rivers where these reservoirs

were impounded (Leite, 1993; Agostinho *et al.*, 1994a; Petrere, 1996; CESP, 1996). The detritivores-illioophages, despite showing a tendency for sharp reduction in most of the six reservoirs, contributed substantially to the post-impoundment catch rate in Jordão Reservoir (26% before, 40% after; by number). Zooplanktivores showed tendencies of colonization in the two reservoirs where they occurred; in Itaipu Reservoir they increased (Agostinho *et al.*, 1994a) and in Rosana Reservoir they remained at low levels (CESP, 1996). Herbivores had sharp increases in abundance in two reservoirs where they occurred (Corumbá Reservoir 13% before, 42% after; Jordão Reservoir 31% before, 47% after), and similar increases were documented in Curuá-Una Reservoir, Amazon River Basin (Ferreira, 1984). In reservoirs where herbivore abundance was low prior to impoundment, their abundance after impoundment remained about the same. This was the case in Três Irmãos (2% before, < 1% after), Rosana (3% before and after), Itaipu (2% before, 3% after), and Tucuruí (4% before, 2% after). Abundance of piscivores increased in Corumbá (10% before, 13% after), Rosana (22% before, 28% after), and Tucuruí (17% before, 46% after), but decreased in Itaipu (27% before, 19% after), and Três Irmãos (33% before, 30% after). Some of these shifts, however, were not substantive.



**Figure 16** Variability in stomach weights before and after impoundment, assessed with residuals from a linear regression analysis between the log of the total weight and stomach weight. After 1 = first year after impoundment; after 2 = second year).

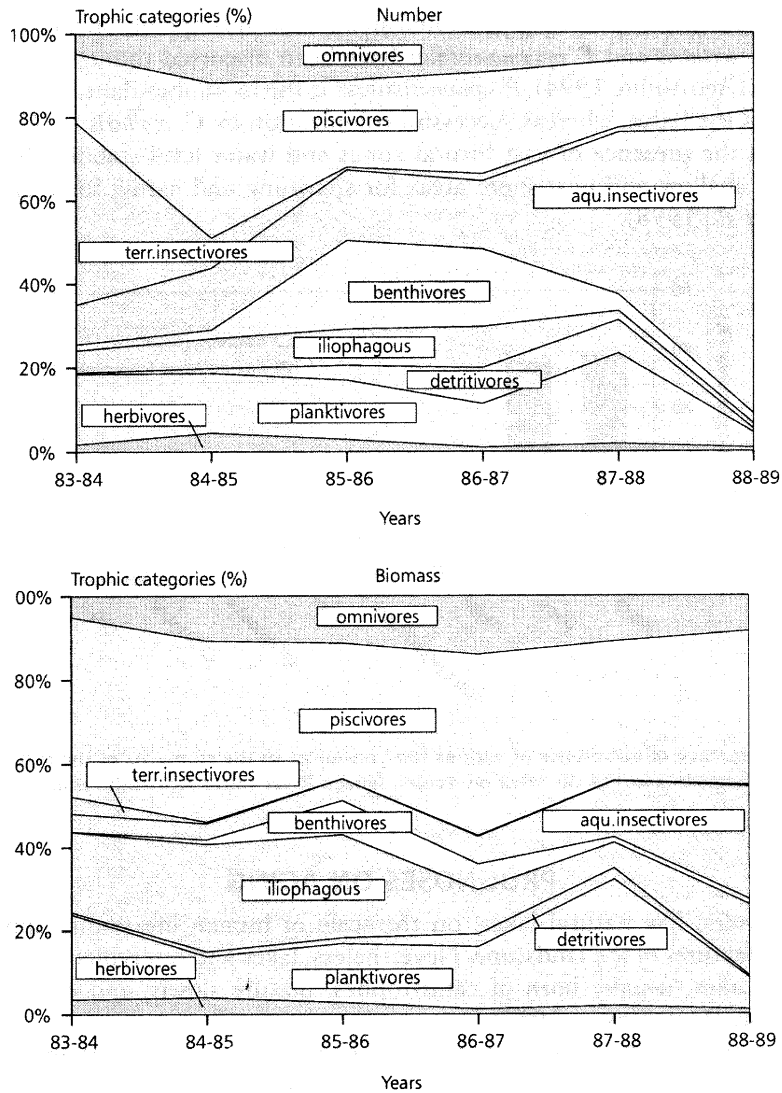
Trophic structure soon after impoundment, considered pivotal for the colonization process (Rodríguez-Ruiz, 1998), seems to depend on two main elements: i) presence of guild elements pre-adapted to lacustrine conditions and with flexible reproductive and feeding strategies, and ii) size of the stock remaining in the reservoir basin. These two elements seem to be more pivotal to colonization than availability of a specific food resource. The high plankton biomass, especially during the trophic upsurge period, has not been capitalized on by adult fishes in large reservoirs of the Upper Paraná River. This is likely a function of the absence of species pre-adapted to pelagic conditions. The success of some herbivores in reservoirs seems to be related to their representation in the fluvial system. Piscivores have become particularly abundant in reservoirs located where pre-adapted lacustrine species were abundant, such as *Cichla* sp. and *Plagioscion* sp. (e.g., Tucuruí Reservoir; Leite, 1993; Petrere, 1996).

Fish communities seem to be sustained mainly by autochthonous resources in older reservoirs. In Itaipu Reservoir, four years after impoundment (Agostinho & Zalewski, 1995), it was estimated that 70% of the fish biomass was composed of species whose diet was based on autochthonous resources (e.g., plankton, benthos, and fish), 25% composed of biomass derived from detritus of mixed origin, and only 5% of the biomass was derived from resources of ecotonal origin (e.g., leaves, fruits, and terrestrial insects). This tendency seems to become more accentuated with time, inasmuch as abundance of planktivores, insectivores, and piscivores have constituted the bulk of the catches in recent years (Figure 17). Benthophages and detritivores (sensu Fugi *et al.*, 1996) exhibited greater densities in the riverine zone of the reservoir, whereas planktophages and illiophages (sensu Fugi *et al.*, 1996), piscivores, and insectivores were more important in the lacustrine zone (Hahn *et al.*, 1998).

Ferreira (1984) analyzed the trophic structure of Curuá-Una Reservoir five years after impoundment, and reported that the dominant trophic groups were herbivores (42% by weight), carnivores (31%), piscivores (26%), and detritivores (1%). Substantial longitudinal variation occurred within the reservoir.

In the Iguaçú River, Segredo and Foz do Areia are contiguous reservoirs, but with different ages. The most pronounced differences in trophic structures of the fish communities in these reservoirs (surveyed when the reservoirs were 1 and 14 years old, respectively) were the composition of detritivores and herbivores. Detritivores were more abundant in Segredo Reservoir (46%) than Foz do Areia Reservoir (6%), herbivores were more abundant in Foz do Areia Reservoir (70%) than Segredo Reservoir (32%) (Agostinho *et al.*, 1997b). Insects and terrestrial plants were the most common items in the diets of fish in these two reservoirs (Figure 18); however, these resources were more important in Foz do Areia Reservoir where they were eaten by 76% of the individuals sampled, than in Segredo Reservoir where they were eaten by 44% (Agostinho *et al.*, 1997b). The high abundance of the herbivore *Astyanax* b contributed to the importance of plants in both reservoirs, especially in Foz do Areia. Insects were present in the diet of all species, except *Hoplias malabaricus*. The importance of insects differed between reservoirs. Hymenoptera was predominant in Foz do Areia, whereas Coleoptera was predominant in Segredo (Agostinho *et al.*, 1997b). Among the other resources, fish and crustaceans had similar contribution to the diets of fish in the two reservoirs, but algae, detritus/sediment, and thecamoebas reduced drastically in importance in the diet of fish in the oldest reservoir. These results suggest that for deep and large reservoirs like Foz do Areia and Itaipu, insects become an important food resource as the reservoir begin to stabilize whereas detritus and algae, important during the trophic upsurge declines.

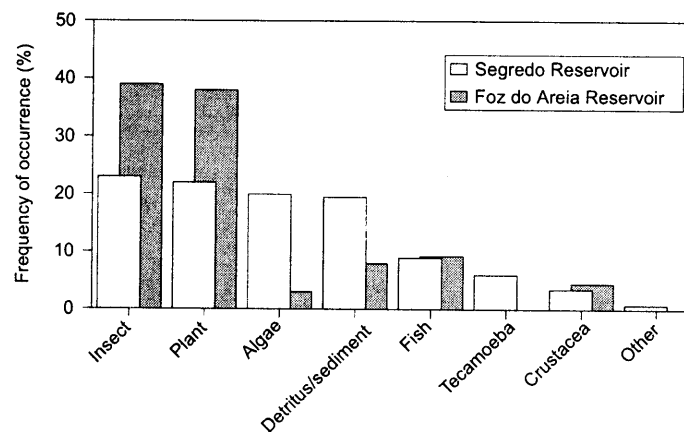
In shallow (< 10 m) and older (> 30 years) reservoirs of the Paraná River Basin the most abundant food seems to be detritus and insects (Arcifa *et al.*, 1988; Arcifa & Meschiatti, 1993; Gehal, 1991), and omnivores the most abundant guild (Araujo-Lima *et al.*, 1995). The primary origin of the detritus is not clear. In Lobo Reservoir (Paraná River Basin), Mozeto *et al.* (1988) reported that detritus originates mainly from macrophytes and tributary inputs. For Tundisi *et al.* (1993), macrophytes are far more important as food for herbivores and detritivores in Amazonian reservoirs.



**Figure 17** Trends in trophic group composition in Itaipu Reservoir (after Hahn *et al.*, 1998). The dam was closed in October 1982.

Productivity and community structure in older reservoirs seem to be affected by density and type of predators. Paiva *et al.* (1994) compared 17 reservoirs in northeastern Brazil, and demonstrated that reservoirs with two predators had higher yields than those with more or fewer predators. This discrepancy was attributed to competition for resources among prey and among predators. Santos *et al.* (1994) analyzed the impact of two introduced piscivores (*Cichla ocellaris* and *Plagioscion squamosissimus*) on zooplankton and prey fish in reservoirs of the Grande River (Paraná River Basin). They concluded

that the presence of both species promoted an increase in zooplankton and a decrease in fish prey. *C. ocellaris* and *P. squamosissimus* have been dispersed throughout the Paraná River Basin (Agostinho, 1994). *P. squamosissimus* is the most abundant predator in large reservoirs of the basin, whereas successful colonization by *C. ocellaris* (= *C. monoculus*) depends on the presence of vast littoral zones and water level stability, because this species use shallow and near-shore areas for spawning and caring for their offspring (Williams *et al.*, 1998).



**Figure 18** Frequency of occurrence of various food resources in the stomachs of the fish assemblages of Segredo and Foz do Areia reservoirs, Iguaçu River (after Agostinho *et al.*, 1997).

### PROGNOSES ON AGING

Reservoirs, like natural lakes, on the scale of human life spans, appear to be permanent features of the landscape. Nevertheless, lakes and reservoirs are geologically transitory. Lakes, usually born of catastrophes, mature slowly, and die quietly and imperceptibly (Hutchinson, 1957).

Reservoirs born from the human need to control the environment, mature rapidly, and do not vanish without a struggle (Pyle, 1995). Unlike natural lakes, reservoirs are likely to be short-lived. Concrete dams will have a geologically-small life span because concrete inevitably deteriorates in about a century, although properly maintained dams may last several centuries (Thomas, 1977). However, it is unlikely that most dams will age much longer than a century because evolving technologies and changing human needs may make dams obsolete, and cost of maintaining aging dams make them an economical liability.

Below we describe the environmental changes associated with reservoir aging, and their interactions with the fish community in the reservoir. Our discussion is severely restricted by the paucity of long-term data sets, and relies heavily on data from temperate



reservoirs because many of them have existed for about half a century, whereas most neotropical reservoirs are not older than a quarter century. We consider this approach justifiable because the main abiotic ingredients of reservoir aging seem consistent between temperate and neotropical latitudes, although relative importance may vary.

### Anticipated Environmental Changes

Aging of lakes and reservoirs is intricately linked to inputs from the watershed. These lentic systems trap and recycle nutrients, organic and silt loads, and even toxic materials. Because reservoirs have a drainage area which is often much larger than that of lakes, and because many are located in rivers draining watersheds with extensive agricultural activities, the effects of loadings are accelerated. Consequently, reservoirs age more rapidly (Kimmel & Groeger, 1986).

Siltation is perhaps the most dominant aging process in reservoirs. The deposition of silt reduces depth, affecting storage capacity of the reservoir and, most importantly, the characteristics of littoral habitats, particularly in embayments. These long-term depth reductions lead to slow changes in bottom firmness, as well as average, minima, and maxima values of temperature, oxygen, and other vital water quality conditions. Silt is likely to be rich in nutrients and organic matter, imported from the drainage area. Both become available for primary production. Ultimately, this production promotes further release of organics and nutrients as they decay, and further eutrophication of the sediments. According to Avnimelech (1989) the accumulation of organic matter in sediments approaches a constant level over time. Reductions in oxygen prompted by decreased depth are exacerbated by increased sediment oxygen demands.

The mean annual rate of storage capacity loss for small temperate reservoirs ( $< 1.23 \cdot 10^5 \cdot \text{m}^3$ ) was estimated at about 2.7% per year (Dendy *et al.*, 1973). At this rate, the average small reservoir would lose half of its storage capacity in about 25 years. Large reservoirs ( $> 1.23 \cdot 10^9 \text{ m}^3$ ) lose storage capacity at an average 0.16% per year (Dendy *et al.*, 1973), implying the average reservoir would lose half of its storage capacity in over 400 years. Thus, large reservoirs have the potential to last several centuries. Nevertheless, because silt deposition progresses from the mouth of the tributaries inward, we suspect that embayments will fill at a rate more similar to that identified for small reservoirs.

As the reservoir ages and siltation progresses, nutrient dynamics of the system begin to change. At higher nutrient levels, phytoplankton communities shift from green to blue-green algae. Although dominance may also shift seasonally, in highly eutrophic reservoirs blue-green algae tend to dominate for a larger portion of the year (Wetzel, 1983). Zooplankton composition is affected by phytoplankton availability. Macrofiltrators (usually large-bodied zooplankton) are more abundant in young, oligotrophic reservoirs, sometimes giving way to low-efficiency, small-bodied, algal and bacterial feeders as reservoir age and nutrients increase (Taylor & Carter, 1998). Eutrophication in Upper Paraná River reservoirs seems to also affect the ratio of calanoid to cyclopoid copepods in the zooplankton community, with the first group becoming predominant over the second one in eutrophic reservoirs (Tundisi *et al.*, 1993). Additionally, in highly eutrophic aging reservoirs the food supply of zooplankton may actually decrease because of the dominance by blue-green algae, which are often inedible

due to their large size (Porter, 1977). These interrelations between phytoplankton and zooplankton can have repercussions throughout the food web. Nevertheless, these changes are likely to occur over long terms. Studies in Paranoá Reservoir have shown that although this reservoir has suffered from gradual nutrient enrichment, over a 13 year period there were no obvious alterations to the zooplankton community (Mattos *et al.*, 1997).

Increased nutrient loads encourage growth of free-floating macrophytes, such as *Eichhornia* spp., whereas depth loss fosters growth of rooted aquatic macrophytes and expand their distribution from shore (Cooke *et al.*, 1993), if water level fluctuations are not too wide. Extensive macrophyte development can control the aquatic ecosystem, beginning with the physical and chemical characteristics of water (e.g., temperature, light, oxygen). Once aquatic macrophytes become established, they can aggravate eutrophic conditions of an aging reservoir through growth-death-decay cycles that allow release of nutrients trapped in sediments, under anaerobic or aerobic conditions.

Another major change induced by aging is the deterioration of habitats, particularly in the littoral zone (Benson, 1982). Standing timber often left in the basin decomposes and falls. Long-term bank erosion induced by wind damage of exposed shorelines turns diverse shoreline habitats into uniform, barren mudflats. In reservoirs with substantial water level fluctuations this effect is not limited to the normal pool shore, but extends into areas above and below normal elevation, and can expand a substantial percentage of the littoral area depending on the slope of the reservoir basin. The original productivity of this ecotone is thereby lost with age, and its instability precludes colonization by terrestrial or aquatic flora.

### **Anticipated Changes in the Fish Communities**

The environmental changes stimulated by aging can have notable repercussions on the fish community of the reservoir. The original period of instability has been associated with the first 5-30 years after impoundment, and appears to be longer at higher latitudes (Balon, 1974; Ploskey, 1981; Benson, 1982; Adams *et al.*, 1983; Lowe-McConnell, 1987). The instability period of neotropical reservoirs is likely to be closer to the lower values in this range, as observed at Itaipu (see above). After this original period, the community is thought as having achieved some climactic level of stability, but changes continue, although at a slower pace.

The stresses induced by long-term changes in environmental conditions associated with aging can lead to a variety of community and species responses, many of which can be anticipated from succession theory. The number of top predators and mean size of species, and even within a species, can be expected to continue to decrease slowly. Often, the most sensitive species are the top predators, and their decline contributes to increased abundance of small prey species. Such declines may be aggravated by elevated fishing pressure stemming from continued expansions in human populations. An increase in planktivorous prey species can lead to a reduction in zooplankton, and thereby increases in algae. Pelagic species will tend to become dominant (e.g., sciaenids) inasmuch as benthic organisms will decline and littoral habitats deteriorate. Short-lived species with fast growth or reproductive compensation (e.g., opportunistic species such as tetragonopterins, and curimatids) will tend to have survival advantages. Shallow, silted

areas colonized by aquatic macrophytes have a dramatic impact on species composition. Generally, as macrophyte density increases, the abundance of pelagic species and benthic omnivores declines (Dibble *et al.*, 1996), and phytophilic species show gains (e.g., erithrinids). These changes increase habitat and species diversity and can be beneficial to fish communities. Nevertheless, as shallow areas and macrophyte coverage become excessive, they can have an overly large effect on water quality and access to food resources, to a point most fish species become extinct, reducing fish species diversity and the value of macrophyte habitats.

The littoral zones seem to be the areas most vulnerable to eutrophication, and coincidentally impacts on these areas have disproportionately large effects on fish communities. Barren, windswept shorelines are poor food producers, unsuitable habitat for nest builders, and poor refuges for juvenile fishes. As the bank and littoral habitats degrade, and environmental conditions or reservoir operation prevent establishment of aquatic macrophytes, density of fish that rely on the littoral zone during all or part of their ontogeny, decreases. In such reservoirs, the fish community shifts towards a dominance by species that can occupy pelagic niches, and thus do not rely on substrates or substrate-based resources. Erosion and ensuing siltation and shallowing of reservoirs has not only been linked to reductions in benthic production, but also to reductions in plankton production through increased water murkiness (Borgström *et al.*, 1992). In advanced stages of aging, fish communities will consist of species (e.g., loricarids and auchenipterids) that thrive in murky, shallow systems, with low oxygen, as documented in Eurasian lakes (Zhakov, 1974).

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