Spatial and temporal gradients in artisanal fisheries of a large Neotropical reservoir, the Itaipu Reservoir, Brazil

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Abstract: Physical, chemical, and biological gradients along reservoirs are clear and exhibit marked spatial and temporal variations. These variations are rarely quantified and may produce spatial gradients in fisheries. We analyzed trends in total yield and gradients and relationships between catch-per-unit-effort (CPUE) and some characteristics of the fishery in the large Neotropical Itaipu Reservoir in Brazil. Data on the artisanal fisheries were collected over an 11-year period (414 213 daily trips). Annual yield (especially after 1993) and CPUE (annual total and for each species) decreased over the studied period. A clear longitudinal pattern in the CPUE values for the main species was recognized, and this pattern presented a significant relationship with the type of gear and characteristics of the vessels used in the fisheries. The decline in yield and CPUE is apparently due to changes in trophic state, as well as to the construction of reservoirs upstream from the region and to overfishing. It is clear that the spatial zonation influenced fish species distribution along the reservoir and, therefore, the fishery. We conclude that for this large Neotropical reservoir, spatial gradient cannot be ignored in management plans, and this appears to be true for any reservoir that exhibits zonation.

Résumé : Il y a des gradients physiques, chimiques et biologiques bien marqués le long des réservoirs et ils présentent de nettes variations dans l'espace et dans le temps. Ces variations sont rarement mesurées quantitativement, bien qu'elles puissent produire des gradients spatiaux dans les pêches. Nous avons analysé les tendances du rendement total et des gradients, ainsi que les relations entre la capture par unité d'effort (CPUE) et quelques caractéristiques de la pêche dans le grand réservoir néotropical Itaipu (Brésil). Les statistiques sur les pêches artisanales ont été compilées sur une période de onze années (414 213 sorties journalières). Le rendement annuel (surtout après 1993) et la CPUE (totale annuelle et spécifique à chaque espèce) ont décliné au cours de la période d'étude. Il existe un net patron longitudinal de CPUE des espèces principales qui est en corrélation significative avec le type d'engin de pêche et les caractéristiques des bateaux utilisés pour la pêche. Le déclin du rendement et de CPUE est apparemment dû à des changements d'état trophique, mais aussi à la construction de réservoirs en amont et à la surpêche. Il est clair que la zonation spatiale influence la répartition des poissons le long du réservoir et, par conséquent, la pêche. En conclusion, on ne peut négliger le gradient spatial dans les plans d'aménagement de ce grand réservoir néotropical; la même contrainte s'impose à tout réservoir qui présente de la zonation.

[Traduit par la Rédaction]

Introduction

Reservoirs are intermediary systems between rivers and natural lakes, the processes in which can be considered more complex and variable. Temporal and spatial variations in water flow through reservoirs can alter, for example, the predominant direction of the axis around which the processes are organized, passing from the vertical (as in lakes) to the horizontal (as in rivers) and vice versa (Noble 1980). In ad-

Received 2 December 2003. Accepted 21 October 2004. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 18 April 2005. J17867

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dition to flow, basin morphometry, circulation pattern, hydraulic retention time, and dam design and operation have a notable influence on the nature, intensity, and duration of the physical and chemical gradients in reservoirs, affecting the structure and dynamics of their biotic communities (Tundisi 1993).

Thornton et al. (1981) described three main zones along a reservoir continuum: the fluvial (including the delta region), transition, and lacustrine zones. These zones can be identified by the sedimentation rate, and their extent is strongly related to the inflow of water and hydraulic retention time. Physical and chemical gradients such as sedimentation rates (Thornton 1990; Pagioro and Thomaz 2002), nutrient concentrations (Tundisi et al. 1988; Kennedy and Walker 1990; Thomaz et al. 1997), and factors related to primary production (Brylinsky and Mann 1973; Hoyer and Jones 1983; Kimmel et al. 1990) have been considered determinants of spatial- and temporal-variation patterns in fish communities (O'Brien 1990; Agostinho et al. 1999*a*) and other communi-

ties (Marzolf 1990; Bini 1997; Nakamoto et al. 1997). Although biotic and abiotic gradients along reservoirs are clear and exhibit marked spatial and temporal variations (Thornton et al. 1990; Gido and Matthews 2000), they are rarely quantified and considered in fishery-management plans.

Spatial and temporal patterns of abiotic or biotic variables verified in reservoirs are expected to influence spatial gradients in fishing systems, including operational fishing strategies, yield, species composition, investments, and profitability. However, the role of spatial gradients has not been explored. Thus, recognition of these patterns and their variations (spatial and temporal) has the potential to support management of fishing resources.

In this study, artisanal-fishery landing data obtained along a large Neotropical reservoir (Itaipu Reservoir) during an 11-year period are analyzed for relationships between catches of the main species and the operational strategies of the fishery along the longitudinal axis of the reservoir. Specifically, the following questions were addressed. (*i*) How do species yields vary temporally (annually) and spatially (along the zones of the reservoir)? (*ii*) Does a relationship exist between yield and the type of gear and the characteristics of the vessels used in the fisheries along the reservoir?

Material and methods

Study area

Itaipu Reservoir, formed in October 1982, is located on the Brazil–Paraguay border, extending for approximately 170 km between 24°05' and 25°33'S and 54°00' and 54°37'W. It has a surface area of 1350 km² and a basin area of approximately 820 000 km². Its average depth is 22 m, reaching 170 m near the dam. Average hydraulic retention is 40 days; however, retention is only 29 days in the main channel. The reservoir was divided into 12 fishing areas (main landing points): (1) Guaíra, (2) Guaíra and vicinity, (3) Oliveira Castro, (4) Arroio Guaçu, (5) Porto Mendes, (6) Pato Bragado, (7) Entre Rios, (8) Santa Helena, (9) Missal, (10) Itaipulândia, (11) São Miguel do Iguaçu, and (12) Santa Terezinha de Itaipu (Fig. 1).

Data collection and analyses

Fishing in Itaipu Reservoir was prohibited for the first 28 months after its formation, and started officially in March 1985. Recording of landings began 2 years later, in January 1987, and continued through December 1998 (except in 1994 (grant interruption)). Reservoir landings (daily catches) from the artisanal fishery were monitored for each species and each fisher, providing a data set of 414 213 daily trips. The information was obtained by a collection network consisting of local people (with experience in the fishery) and organizations, such as fishing associations. Fishing effort was represented by the number of days (trips) fished, expressed at the specific level for each fishery area. Yield was presented as CPUE (kg·fisher⁻¹·day⁻¹).

Firstly, we characterized the fishery at Itaipu Reservoir in terms of changes in total yield (tons (t)) and CPUE along the years studied and of the species that contributed most to the landings (90% of the total). Secondly, we examined the adequacy of the zonation (fluvial, transition, and lacustrine zones) described by Pagioro and Thomaz (2002) for the fishery conducted at Itaipu Reservoir. To achieve this, we used a multivariate analysis technique to reduce data dimensionality, and then, using detrended correspondence analysis (DCA), summarized the longitudinal gradient of yield based on the CPUE values of only the species that contributed to 90% of the landings because rare species may have a disproportionate influence on DCA results (Palmer 1993). Axes with eigenvalues above 0.20 were retained for interpretation (ter Braak and Šmilauer 1998). Axis sample scores for each fishing area were retained for interpretation and plotted against the sedimentation rates found by Pagioro and Thomaz (2002) along the reservoir. A Spearman's rank correlation (r_s) was then used to test the adequacy of the zones, i.e., the association between the sedimentation rates and scores of the DCA axes retained for interpretation, which in turn synthesized the variations in yield of the main species.

To evaluate spatial and temporal variations in the CPUE values for the main species along the longitudinal axes of the reservoir, fishing areas were grouped into the previously identified zones (fluvial, transition, and lacustrine), and twoway analyses of variance (ANOVAs) were applied using zone and year as factors. As several ANOVAs were applied (most abundant species), we used the protected ANOVA protocol to minimize Type I error (Scheiner 1993). In accordance with this protocol, a two-way multivariate analysis of variance (MANOVA) was applied considering the main species before the ANOVAs. If the MANOVA is significant, then ANOVAs can be applied (for each species separately). CPUE values were log-transformed (log(CPUE + 1)) to meet assumptions of the tests.

During the sampling period, information related to type of gear (operational fishing strategy) and vessel used was collected. Information related to gear type consisted of the number of fishers that used gillnets, long lines, cast nets, and other gear (e.g., a hook and line attached to a float, set near macrophyte stands, like a jug line, locally named espera, used to catch mainly the traíra (Hoplias malabaricus), and similar gear, but with larger hooks, that drifts in the reservoirs, locally named cavalinho, which targets the barbado (Pinirampus pirinampu)). Vessel characteristics included paddle, stationary (center) engine (10–12.5 h.p. (1 h.p. = 746 W)), outboard engine, and "rabeta" engine (3.5–4.5 h.p.). These data, obtained for each fishery area, were logtransformed $(\log(x + 1))$ and analyzed using principal components analysis (PCA) to reduce dimensionality. Axes that presented eigenvalues greater than those produced by the randomness hypothesis of the broken-stick model were retained for interpretation (Jackson 1993). Pearson's correlations (r) were determined between the DCA and PCA axes retained for interpretation to evaluate the relationship between main-species yields and the types of gear and vessel characteristics.

Results

Temporal variations in the fishery

Annual yield from 1987 to 1998 fluctuated between 1727 t (1989) and 1192 t (1998), remaining almost constant from 1987 to 1993. The average CPUE values, high in the initial years of exploitation (e.g., 21.7 kg·fisher⁻¹·day⁻¹ in 1987), decreased over time, with values of 15.5 kg·fisher⁻¹·day⁻¹



Fig. 1. Map of Itaipu Reservoir (Brazil-Paraguay border) showing the longitudinal gradient (fluvial, transition, and lacustrine zones) and fishery areas.

Fig. 2. Temporal variations in (*a*) catch-per-unit-effort (CPUE) in the artisanal fishery of Itaipu Reservoir (vertical lines represent standard error) and (*b*) total annual yield in tons (t).



from 1990 to 1992 and about 11.5 kg·fisher⁻¹·day⁻¹ from 1995 to 1998 (Fig. 2). The main species caught in the artisanal fishery during the period, in order of decreasing abundance, were perna-de-moça (*Hypophthalmus edentatus*), armado (*Pterodoras granulosus*), curvina (*Plagioscion squamosissimus*), curimba (*Prochilodus lineatus*), mandi (*Pimelodus maculatus*), mandi-prata (*Iheringichthys labrosus*), cascudo-preto (*Rhinelepis aspera*), *P. pirinampu*, *H. malabaricus*, and jaú (*Paulicea luetkeni*), which together composed approximately 90% of the landings.

Spatial gradients in CPUE

Application of DCA to the CPUE data revealed that the first axis presented eigenvalues greater than 0.20 ($\lambda = 0.27$) and therefore was retained for interpretation. The spatial distribution of the scores on axis 1 of the DCA (DCA1) is consistent with variations in sedimentation rates (Spearman's rank correlation, $r_{\rm S} = 0.77$, P = 0.0034). Sedimentation rates were high in the fluvial zone, intermediate in the transition zone, and low in the lacustrine zone (Fig. 3; for details see Pagioro and Thomaz 2002). Therefore, the spatial distribution of the scores on axis 1 showed a clear longitudinal gradient, which allowed separation into the zones identified by Pagioro and Thomaz (2002) (Fig. 3). The fluvial zone includes the fishery areas of Guaíra, Guaíra and vicinity, and Oliveira Castro and is located in the first 25 km of the reservoir. The transition zone comprises the fishery areas of Arroio Guaçu, Porto Mendes, and Pato Bragado and extends

Fig. 3. Scatterplot of detrended correspondence analysis axis 1 (DCA1) scores applied to CPUE values for the 10 main species in the artisanal fishery landings and the sedimentation rates along Itaipu Reservoir (\blacksquare , fluvial zone; +, transition zone; ●, lacustrine zone; \diamondsuit , sedimentation rate). Spearman's r = 0.77, P = 0.0034, n = 12. DW, dry weight.



approximately for 35 km. The lacustrine zone is in the interior and extends for 90 km, comprising the fishery areas of Entre Rios, Santa Helena, Missal, Itaipulândia, São Miguel do Iguaçu, and Santa Terezinha de Itaipu (see Fig. 1).

MANOVA applied to the yield of the main species, with zone and year as independent factors, showed significant differences (R of Rao (Linderman et al. 1980; Rao 1952; Tatsuoka 1971): $zone_{[6,722]} = 25.18$, $year_{[30,1060]} = 2.90$, zone × year_{160,10781} = 1.80, all with P < 0.0001), indicating the relevance of applying ANOVAs for each species. For the separate ANOVAs, interactions were significant $(F_{[20,363]} > 2.20)$ and P < 0.01) for P. squamosissimus and P. maculatus, indicating that the yields of these species varied among the zones and years considered (Table 1; Fig. 4). Yields of H. malabaricus and I. labrosus varied only among years $(F_{[2,363]} > 2.60 \text{ and } P < 0.01)$, whereas *R. aspera* yields varied among zones ($F_{[10,363]} = 43.43$ and P < 0.001) (Table 1; Fig. 4). For the other species (P. granulosus, H. edentatus, P. pirinampu, P. luetkeni, and P. lineatus), patterns of yield were clearer because both factors were significant (F > 2.10and *P* < 0.03; Table 1; Fig. 4).

The two main species comprised almost half of all fish landings during the years analyzed (H. edentatus 22.3% and P. granulosus 22.1%). They showed obvious longitudinal gradients in abundance (Table 1; Fig. 4). Catches of H. edentatus, a zooplanktivorous filter feeder, occurred essentially in the lacustrine and transition zones. Temporal variations, also significant, were especially evident in the lacustrine zone, where CPUE values for H. edentatus in the initial years of exploitation were approximately double those in the transition zone; after 1993, however, CPUE values in the lacustrine zone were below those in the transition zone (although CPUE in the transition zone was less variable over the period). Pterodoras granulosus, an omnivore more abundant in the fisheries of the fluvial zone, also exhibited marked annual variation in catches (Table 1; Fig. 4), with a peak in CPUE in the fluvial zone in 1989 and an increase in the transition zone starting in 1993. Among the most abun-

	Zone		Year		Zone \times year	
	$\overline{F_{[2]}}$	Р	$F_{[10]}$	Р	F _[20]	Р
Pterodoras granulosus	257.35	< 0.001	2.83	0.004	1.54	0.084
Hypophthalmus edentatus	86.39	< 0.001	2.15	0.027	1.33	0.176
Pinirampus pirinampu	58.35	< 0.001	2.88	0.003	0.81	0.691
Rhinelepis aspera	43.43	< 0.001	1.40	0.191	1.15	0.312
Paulicea luetkeni	23.73	< 0.001	4.72	< 0.001	0.57	0.922
Prochilodus lineatus	13.36	< 0.001	6.09	< 0.001	0.93	0.548
Plagioscion squamosissimus	6.32	0.003	6.42	< 0.001	4.48	< 0.001
Pimelodus maculatus	4.73	0.011	1.02	0.429	2.30	0.004
Hoplias malabaricus	1.99	0.143	2.64	0.007	1.33	0.180
Iheringichthys labrosus	0.47	0.624	2.88	0.003	1.00	0.473

Table 1. Two-way analysis of variance (ANOVA) applied to the catch-per-unit-effort (CPUE; kg·fisher⁻¹·day⁻¹) data for the main species, with reservoir zone and year as factors.

Note: Numbers in boldface type are significant at P < 0.05; F, Fisher's statistic; P, probability of finding a greater

F value; zone \times year, interaction of zone and year.

dant species, the piscivorous *P. squamosissimus* is the only one that is introduced (from the Amazon basin). During the period, it yielded more or less constant CPUE values in the fluvial and lacustrine zones. However, catches of this species in the fluvial zone, formerly superior to catches of the other species, decreased markedly over the years studied (8.2 kg·fisher⁻¹·day⁻¹ in 1987, 0.9 kg·fisher⁻¹·day⁻¹ in 1998), with conspicuous decreases in 1991 and 1995.

The other species with significant differences in longitudinal gradients were all large migratory species. Of these, *P. pirinampu*, *P. maculatus*, and *P. lineatus* were more abundant in the fluvial and transition zones, whereas *R. aspera* and *P. luetkeni* were caught essentially in the fluvial zone. The sedentary species *H. malabaricus* and *I. labrosus* showed no clear patterns of variation in CPUE along the longitudinal axis of the reservoir, with capture peaks alternating between the zones. The latter species, however, showed high CPUE values in 1993 and 1997 but with great variations in averages. Overall, reductions in total fishery yield were not uniform along the reservoir. They were more conspicuous in the lacustrine and fluvial zones, whereas mean yields in the transition zone fluctuated less during the period (Fig. 5).

Spatial gradients in the fisheries and relationship with gear type and vessel characteristics

Two PCA axes presented eigenvalues greater than the broken-stick eigenvalues, and they were retained for interpretation. These two components explained 71.6% of the variability in fishing strategies related to gear type and vessels used in the reservoir (Table 2). Variables that most contributed to the first PCA axis (PC1) were cast nets and stationary engine (positively) and rabeta engine, gillnets, and paddle (negatively). For PC2, long lines were the most negatively correlated variable. Significant correlations between DCA1 (which summarized the CPUE values for the most important species) and PC1 and PC2 (which summarized gear type and vessel characteristics) were observed (Table 2). These significant correlations demonstrate an association between DCA and PCA. Therefore, it can be inferred that negative scores on PC1 were associated with gear type and vessel used in the H. edentatus fishery (represented by the low DCA scores), i.e., the use of gillnets and boats driven by paddle and rabeta engines in the more interior regions of the reservoir. Positive scores on PC1 were associated with the use of cast nets and a stationary engine, mainly in the *R. aspera* fishery and, to a lesser degree, in the *P. granulosus* fishery in the upper stretches of the reservoir, especially Guaíra and vicinity (Fig. 6a). The association of the *P. granulosus* fishery and, to a lesser degree, the *P. luetkeni* fishery with the use of long lines and a stationary engine in the fluvial zone, especially in Guaíra and vicinity, is better visualized when the relationship between DCA1 and PC2 is analyzed (Fig. 6b).

Discussion

Daily monitoring of landings and effort of the artisanal fishery, carried out over 11 years, allowed the characterization of variations in the spatial and temporal dynamics of the exploited stocks in Itaipu Reservoir. The fishery declined markedly during the analyzed period. This decline can be attributed mainly to alterations in trophic state over the years (i.e., a trophic upsurge, a general occurrence in reservoirs; Kimmel and Groeger 1986; Petrere 1996; Williams et al. 1998).

In general, the release of nutrients immediately following reservoir closure leads to increases at all trophic levels (O'Brien 1990) and there is a high availability of food resources for fish in the new environment, although extensive anoxic areas may be formed, temporarily restricting colonization by the original communities. These conditions lead to processes that select species with high physiological tolerance and behavioral plasticity that, using the abundant resources, proliferate and reach high biomass levels (Lowe-McConnell 1987; Agostinho et al. 1999a). The heterotrophic phase, however, ends with mineralization of the flooded organic material, and resources become essentially autochthonous (Petrere 1996). This leads to population alterations and, consequently, modifications in stocks of exploited fish. However, the effects of these events in fish communities are difficult to predict inasmuch as reservoirs are managed environments and responses of communities to a given disturbance may be aborted before completion (Agostinho et al. 1999a). The result is a chaotic succession of reactions marked by a reduction in interdependence between species and low biotic

Fig. 4. Spatial and temporal variations in yields (CPUE) of the main species, (a) Hypophthalmus edentatus, (b) Plagioscion squamosissimus, (c) Pimelodus maculatus, (d) Iheringichthys labrosus, (e) Hoplias malabaricus, (f) Pterodoras granulosus, (g) Prochilodus lineatus, (h) Rhinelepis aspera, (i) Pinirampus pirinampu, and (j) Paulicea luetkeni, from the artisanal fisheries of Itaipu Reservoir (vertical lines represent standard error; \blacksquare , fluvial zone; +, transition zone; ●, lacustrine zone).



Year

34

30

26

Fig. 5. Temporal variations in CPUE in the artisanal fishery of Itaipu Reservoir according to the longitudinal gradient (vertical lines represent standard error: . fluvial zone: +, transition zone: •, lacustrine zone).

CPUE (kg·fisher ¹·day ¹) 22 18 14 10 6 1987 1988 1989 1990 1991 1992 1993 1995 1996 1997 1998 Year

stability, altering the biota and the succession process (Wetzel 1990).

In addition to changes in trophic state, operation of the upstream reservoirs (in some years in association with low precipitation) greatly affects the flood regime of the Paraná River floodplain, with a direct influence on the fishery. Six out of the 10 species that sustain the Itaipu Reservoir fishery are large migratory species that use the free stretches of the basin above the reservoir (230 km) for spawning and the floodplain for their initial development (Agostinho et al. 2001). Gomes and Agostinho (1997) observed high correlations between the flood regime of the upper Paraná River floodplain and the yield of P. lineatus in the reservoir, fry of this species having stayed in floodplain lagoons for 2 years. Agostinho et al. (2004), monitoring marginal lagoons along the free stretch of the Paraná River, observed that the density of juveniles of the most migratory species that make up the reservoir fishery is related to the duration and period of floods. These authors give an account of the absolute absence of juveniles of migratory species in the years in which waters of the Paraná River did not reach the floodplain.

Processes of transport and deposition of sediments are important forces in determining spatial (longitudinal) gradients in reservoirs (Thornton 1990; Kimmel et al. 1990). Patterns of variation in sedimentation rate in Itaipu Reservoir were consistent with spatial variations in catches of the main species of the artisanal fishery (summarized by DCA1), allowing recognition of zonation. Spatial gradients were insignificant only for H. malabaricus and I. labrosus, two sedentary species that inhabit the littoral areas of the entire reservoir and complete their life cycles there. The first species is essentially piscivorous, builds littoral refuges, and provides parental care, whereas the second has a benthivorous diet, feeding on aquatic invertebrates in shallow areas (Hahn et al. 1998). Both have shown significant increases in abundance in recent years. This is attributed to the relative stability in the level of the reservoir.

The other two species restricted to the reservoir areas (H. edentatus and P. squamosissimus) exhibited significant spatial and temporal variations in abundance. Hypophthalmus edentatus, the main species in the fishery during the en-

Table 2. Eigenvectors of axes 1 and 2 of the principal components analysis (PCA) applied to the gear type and vessel characteristics data matrix, eigenvalues (for each axis and the brokenstick), percent explanation of the axes retained for interpretation, and Pearson's correlation values between PCA axes and axis 1 of the detrended correspondence analysis (DCA1).

Eigenvector	Axis 1	Axis 2
Gillnets	-0.4351	-0.2996
Long lines	0.0894	-0.5326
Cast nets	0.3612	-0.4022
Others	-0.0317	-0.4932
Paddle	-0.4322	-0.1384
Stationary engine	0.3342	-0.3934
Outboard motor	-0.3746	-0.1983
"Rabeta" motor	-0.4820	-0.0917
Eigenvalues (broken-stick)	3.459 (2.718)	2.272 (1.718)
Percent explanation	43.24	28.4
Pearson's correlation with	0.614 (<0.001)	-0.472 (<0.001)
DCA1		

tire period, occupied mainly the interior pelagic areas of the reservoir, principally the lacustrine zone. Its stock in the reservoir is decreasing, however, as is demonstrated by the annual CPUE variations. Although alterations in the diet of this species have been slight over the last 10 years (Ambrosio et al. 2001), with substitution of bosminid for daphniid cladocerans as the dominant item in its diet, it is probable that the change in trophic state of the reservoir has affected food availability for the species. In this sense, flow regulation and nutrient retention by the new reservoirs upstream probably made an important contribution through the expected effects on productivity in Itaipu Reservoir, mainly in the more interior lacustrine areas (the abundance of H. edentatus in the transition zone remained constant during the study period).

Plagioscion squamosissimus, the adults of which prey intensively on the annual fry of H. edentatus (Hahn et al. 1997), is the main piscivore in the Itaipu Reservoir fish landings. Its abundance showed little variability in the transition and lacustrine zones; however, it presented a marked decline in the fluvial zone, where it had been concentrated in the first 4 years of the study period. The predator-prey interactions between these two species, allied with changes in trophic state, seem to be the most appropriate explanation for the decline of both.

Rhinelepis aspera, P. luetkeni, and P. granulosus, which preferentially inhabit the bottom (Freire and Agostinho 2001), were typical of the fluvial zone. Prochilodus lineatus, P. pirinampu, and P. maculatus, which have little association with the lower portions of the water column, were more abundant in the transition zone. These six species can be categorized into three distinct trophic groups (Hahn et al. 1997): detritivorous (R. aspera and P. lineatus), omnivorous (P. granulosus and P. maculatus), and piscivorous (P. pirinampu and P. luetkeni). They are able to use the transported allochthonous food resources that enter both zones and small prey that are abundant in the entire reservoir (Benedito-Cecílio and Agostinho 1999). The important sedentary species in the fishery (with and without spatial gradients in the

Fig. 6. Ordination of the data on type of gear and vessel characteristics in Itaipu Reservoir (significant axes of the principal components analysis axis 1 (PC1; *a*) and axis 2 (PC2; *b*) in relation to the variations in catch of the main species (DCA1). The number above each symbol indicates the fishing area (see "Study area") (\blacksquare , fluvial zone; +, transition zone; \bigcirc , lacustrine zone).



catches) fed essentially on autochthonous resources (plankton and aquatic invertebrates, in addition to fish).

Four of the six migratory species (*P. granulosus*, *R. aspera*, *P. lineatus*, and *P. luetkeni*) showed a decline in catches in the fluvial zone because of multiple factors, especially local overfishing (*R. aspera*; Okada et al. 1996) and flood regulation on the upper Paraná River floodplain. The tendency towards depletion in the artisanal fishery, involving all species, reflects spatial and temporal variations of the main species, particularly declines in catches of *H. edentatus* in the lacustrine zone and *P. granulosus* in the fluvial zone. CPUE values were constant in the transition zone but decreased in the others. The fact that the fluvial and lacustrine zones contained species with distinct environmental demands, and whose distributions overlapped in the transition zone, suggests that the decrease in total fishing yield over the period could be a result of distinct adverse factors.

Longitudinal gradients in the abundance and composition of the catches reflect the degree of dependence of the species on the lentic conditions in the reservoir (availability of autochthonous resources, water transparency) and the lotic condition in the river (availability of allochthonous resources, turbidity, and water circulation), both mainly determined by the processes of transport and sediment deposition. Fishing strategies, on the other hand, are dependent on intrinsic components of local stocks (specific composition, feeding behavior, microhabitat) and the environment (water velocity and turbidity), in addition to cultural (fishing tradition and empirical knowledge) and socioeconomic (specific demand, cost, profitability, investment capacity) aspects. Understanding the dynamics of these factors, besides those of the resource itself, is fundamental to the delineation of management strategies (Hilborn and Walters 1992). However, the heterogeneity with which they are presented in a multispecific fishery such as that of Itaipu Reservoir makes analysis of this fishery-system component a complex task. The use of a multivariate approach seems, however, promising (Pelletier and Ferraris 2000). In this study, spatial variations in some of these variables were satisfactorily summarized. Spatial variations in the type of gear used and vessel characteristics, summarized on the first two PCA axes, were plotted against variations in catches of the main species, summarized on the first DCA axis. This analysis made it possible to identify patterns in the capture of at least three of the main species.

The *R. aspera* fishery is typical of the fluvial zone (Guaíra) and is carried out using cast nets. This species lives on irregular rocky bottoms in depths of up to 6 m at the entrance of the reservoir (Delariva and Agostinho 2001). Wooden boats propelled by a stationary engine strong enough to overcome the more rapid currents in the region are used (Okada et al. 1996). Fisheries of *P. granulosus* and *P. luetkeni*, species more abundant in the fluvial zone, also involve the use of a wooden boat propelled by a stationary engine and long lines. On the other hand, gillnets capture *H. edentatus* in the more interior zones, with the use of wooden boats propelled by paddle or a rabeta engine. These types of propulsion are suitable in these zones because of low water velocities and low operational costs of the boat (Okada et al. 1997).

Although it can be considered low-yield when compared with similar environments in other basins (Marshall 1984; Paiva et al. 1994; Gomes and Miranda 2001), the Itaipu Reservoir fishery plays an important social and economic role for a great number of fishers who, in general, would not have any alternative legal employment, inasmuch as most have been marginalized by other productive sectors of the economy. Carried out in a border area (Brazil–Paraguay) where illicit activities such as smuggling, drug trafficking, and transporting stolen vehicles across the border are common practices, the fishery in this reservoir needs increased government attention to address the tendency towards successive yield decreases that threaten to push these fishers to the brink of absolute marginality.

The decline in yield of Itaipu Reservoir appears to be mainly due to a change in trophic state, which is a common occurrence in reservoirs (Kimmel and Groeger 1986; Petrere 1996). However, in this reservoir, other factors may be worsening the situation, such as the construction of reservoirs upriver (Agostinho et al. 2004) and overfishing (Okada et al. 1996; Agostinho et al. 1999*b*; Miranda et al. 2000). It is also evident that the longitudinal gradients in the reservoir identified by Pagioro and Thomaz (2002) influence fish species distribution along the reservoir and, consequently, the fishery. Therefore, these longitudinal gradients should be considered in any management plan. Ignorance of the existence of these gradients led, for example, to the construction of infrastructures to support the fishery in the inner part of another reservoir (Sobradinho Reservoir, São Francisco River), which later became less productive (Agostinho 1998).

Acknowledgements

We thank Dr. Luiz Maurício Bini for helping in the statistical analysis of the data, Dr. Harumi Irene Suzuki for reviewing the text and making suggestions, University employees Vanderlei Pereira da Silva and Maria de Lourdes Batista Nunes and Dr. Angela Maria Ambrósio for helping in the field collection and laboratory analyses, and David Hoeinghaus for his suggestions and English improvements. This study was carried out with the financial support of Itaipu Binacional and Nupélia, Universidade Estadual de Maringá.

References

- Agostinho, A.A. 1998. A pesca no reservatório de Sobradinho : considerações sobre a pesca no reservatório de Sobradinho e ações recomendadas para sua otimização. Universidade Estadual de Maringá – Nupélia, Maringá, Brazil, Tech. Rep. 1998.
- Agostinho, A.A., Miranda, L.E., Bini, L.M., Gomes, L.C., Thomaz, S.M., and Suzuki, H.I. 1999a. Patterns of colonization in neotropical reservoirs, and prognoses on aging. *In* Theoretical reservoir ecology and its applications. *Edited by* J.G. Tundisi and M. Straškraba. International Institute of Ecology, São Carlos, Brazil. pp. 227–265.
- Agostinho, A.A., Okada, E.K., and Gregoris, J. 1999b. A pesca no reservatório de Itaipu : aspectos sócioeconômicos e impactos do represamento. *In* Ecologia de reservatórios: estrutura, função e aspectos sociais. *Edited by* R. Henry. Fundação de Amparo à Pesquisa do Estado de São Paulo / Fundação do Instituto de Biociências (FUNDIBIO/FAPESP), Botucatu, São Paulo, Brazil. pp. 279–320.
- Agostinho, A.A., Gomes, L.C., and Zalewski, M. 2001. The importance of floodplains for the dynamics of fish communities of the upper river Paraná. Ecohydrol. Hydrobiol. 1(1–2): 209–217.
- Agostinho, A.A., Gomes, L.C., Veríssimo, S., and Okada, E.K. 2004. Flood regime, dam regulation and fish in the upper Paraná River: effects on assemblage attributes, reproduction and recruitment. Rev. Fish Biol. Fish. 14(1): 11–19.
- Ambrosio, A.M., Agostinho, A.A., Gomes, L.C., and Okada, E.K. 2001. The fishery and fishery yield of *Hypophthalmus edentatus* (Spix. 1829), (Siluriformes, Hypophthalmidae), in the Itaipu reservoir, Paraná state, Brazil. Acta Limnol. Bras. **13**(1): 93–105.
- Benedito-Cecílio, E., and Agostinho, A.A. 1999. Determination of patterns of ichthyofauna co-occurrence in the Paraná river basin, area of influence of the Itaipu reservoir. Interciência, **24**(6): 360–365.
- Bini, L.M. 1997. Spatial variation of some limnological parameters in Barra Bonita reservoir (São Paulo, Brazil): a geostatistical approach. Verh. Int. Ver. Theor. Angew. Limnol. 26: 229–231.
- Brylinsky, M., and Mann, K.H. 1973. An analysis of factors governing productivity in lakes and reservoirs. Limnol. Oceanogr. **18**(1): 1–14.

- Delariva, R.L., and Agostinho, A.A. 2001. Relationship between morphology and diets of six neotropical loricariids. J. Fish Biol. 58: 832–847.
- Freire, A.G., and Agostinho, A.A. 2001. Ecomorfologia de oito espécies dominantes da ictiofauna do reservatório de Itaipu (Paraná/Brasil). Acta Limnol. Bras. **13**(1): 1–9.
- Gido, K.B., and Matthews, W.J. 2000. Dynamics of the offshore fish assemblage in a southwestern reservoir (Lake Texona, Oklahoma–Texas). Copeia, **4**: 917–930.
- Gomes, L.C., and Agostinho, A.A. 1997. Influence of the flooding regime on the nutritional state and juvenile recruitment of the curimba, *Prochilodus scrofa*, Steindachner, in upper Paraná river, Brazil. Fish. Manag. Ecol. 4(4): 263–274.
- Gomes, L.C., and Miranda, L.E. 2001. Riverine characteristics dictate composition of fish assemblages and limit fisheries in reservoirs of the upper Paraná River Basin. Regul. Rivers Res. Manag. 17: 67–76.
- Hahn, N.S., Agostinho, A.A., and Goiten, R. 1997. Feeding ecology of curvina *Plagioscion squamosissimus* (Heckel, 1840) (Osteichthyes, Perciformes) in the Itaipu reservoir and Porto Rico floodplain. Acta Limnol. Bras. 9: 11–22.
- Hahn, N.S., Agostinho, A.A., Gomes, L.C., and Bini, L.M. 1998. Estrutura trófica da ictiofauna do reservatório de Itaipu (Paraná– Brasil) nos primeiros anos de sua formação. Interciência, 23(5): 299–305.
- Hilborn, R., and Walters, C.J. (*Editors*). 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.
- Hoyer, M.V., and Jones, J.R. 1983. Factors affecting the relationship between phosphorus and chlorophyll *a* in Midwestern reservoirs. Can. J. Fish. Aquat. Sci. 40: 192–199.
- Jackson, D.A. 1993. Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. Ecology, 74(8): 2204–2214.
- Kennedy, R.H., and Walker, W.W. 1990. Reservoir nutrient dynamics. *In* Reservoir limnology: ecological perspectives. *Edited by* K.W. Thornton, B.L. Kimmel, and F.E. Payne. John Wiley & Sons, New York. pp. 109–131.
- Kimmel, B.L., and Groeger, A.W. 1986. Limnological and ecological changes associated with reservoir aging. *In* Reservoir Fisheries Management: Strategies for the 80's: Proceedings of a National Symposium on Managing Reservoir Fishery Resources, June 1983, Lexington, Kentucky. *Edited by* G.E. Hall and M.J. Van Den Avyle. Reservoir Committee Southern Division, American Fisheries Society, Bethesda, Md. pp. 103–109.
- Kimmel, B.L., Lind, O.T., and Paulson, L.J. 1990. Reservoir primary production. *In* Reservoir limnology: ecological perspectives. *Edited by* K.W. Thornton, B.L. Kimmel, and F.E. Payne. John Wiley & Sons, New York. pp. 133–193.
- Linderman, R.H., Merenda, P.F., and Gold, R. 1980. Introduction to bivariate and multivariate analysis. Scott, Foresman and Co., New York.
- Lowe-McConnell, R.H. 1987. Ecological studies in tropical fish communities. Cambridge University Press (Cambridge Tropical Biology Series), Cambridge.
- Marshall, B.E. 1984. Predicting ecology and fish yields in African reservoirs from preimpoundment physico-chemical data. Committee for Inland Fisheries of Africa, Food and Agriculture Organization, Rome. Tech. Pap. No. 12.
- Marzolf, G.R. 1990. Reservoirs as environments for zooplankton. *In* Reservoir limnology: ecological perspectives. *Edited by* K.W. Thornton, B.L. Kimmel, and F.E. Payne. John Wiley & Sons, New York. pp. 195–208.

- Miranda, L.E., Agostinho, A.A., and Gomes, L.C. 2000. Appraisal of the selective properties of gill nets and implications for yield and value of the fisheries at the Itaipu Reservoir, Brazil–Paraguay. Fish. Res. (Amst.), 45: 105–116.
- Nakamoto, N., Tundisi, J.G., Marins, M.A., and Godinho, M.J.L. 1997. Longitudinal distribution of plankton in a shallow reservoir of Broa in Brazil. Verh. Int. Ver. Theor. Angew. Limnol. 26(2): 553–557.
- Noble, R.L. 1980. Management of lakes, reservoirs and ponds. *In* Fisheries management. *Edited by* R.T. Lackey and L.A. Nielsen. Blackwell Scientific Publications, Oxford and London. pp. 265– 295.
- O'Brien, W.J. 1990. Perspectives on fish in reservoir limnology. *In* Reservoir limnology: ecological perspectives. *Edited by* K.W. Thornton, B.L. Kimmel, and F.E. Payne. John Wiley & Sons, New York. pp. 209–225.
- Okada, E.K., Agostinho, A.A., and Petrere Júnior, M. 1996. Catch and effort data and the management of the commercial fisheries of Itaipu reservoir in the upper Paraná River, Brazil. *In* Stock assessment in inland fisheries. *Edited by* I.G. Cowx. Fishing News Books, Oxford. pp. 154–161.
- Okada, E.K., Gregoris, J., Agostinho, A.A., and Gomes, L.C. 1997. Diagnóstico da pesca profissional em dois reservatórios do rio Iguaçu. *In* Reservatório de Segredo : bases ecológicas para o manejo. *Edited by* A.A. Agostinho and L.C. Gomes. Editora da Universidade Estadual de Maringá, Maringá, Paraná, Brazil. pp. 293–318.
- Pagioro, T.A., and Thomaz, S.M. 2002. Longitudinal patterns of sedimentation in a deep, monomictic subtropical reservoir (Itaipu, Brazil–Paraguay). Arch. Hydrobiol. 154(3): 515–528.
- Paiva, M.P., Petrere Junior, M., Petenate, A.J., Nepomuceno, F.H., and Vasconcelos, E.A. 1994. Relationship between the number of predatory fish species and fish yield in large northeastern Brazilian reservoirs. *In* Rehabilitation of freshwater fisheries. *Edited by* I.G. Cowx. Fishing News Books, Oxford. pp. 120–130.
- Palmer, M.W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology, 74: 2215– 2230.
- Pelletier, D., and Ferraris, J. 2000. A multivariate approach for defining fishing tactics from commercial catch and effort data. Can. J. Fish. Aquat. Sci. 57: 51–65.
- Petrere, M. 1996. Fisheries in large tropical reservoirs in South America. Lakes Reserv. Res. Manag. 2: 111–133.
- Rao, C.R. 1952. Advanced statistical methods in biometric research. Wiley, New York.
- Scheiner, S.M. 1993. MANOVA: multiple response variables and multispecies interactions. *In* Design and analysis of ecological experiments. *Edited by* S.M. Scheiner and J. Gurevitch. Chapman & Hall, New York. pp. 94–112.
- Tatsuoka, M.M. 1971. Multivariate analysis. Wiley, New York.
- ter Braak, C.J.F., and Šmilauer, P. 1998. Reference manual and user's guide to CANOCO for Windows: software for canonical community ordination. Version 4 [computer program]. Microcomputer Power, Ithaca, N.Y.
- Thomaz, S.M., Bini, L.M., and Alberti, S.M. 1997. Limnologia do reservatório de Segredo : padrões de variação espacial e temporal. *In* Reservatório de Segredo : bases ecológicas para o manejo. *Edited by* A.A. Agostinho and L.C. Gomes. Editora da Universidade Estadual de Maringá, Maringá, Paraná, Brazil. pp. 19–37.
- Thornton, K.W. 1990. Sedimentary processes. *In* Reservoir limnology: ecological perspectives. *Edited by* K.W. Thornton, B.L. Kimmel, and F.E. Payne. John Wiley & Sons, New York. pp. 43–69.

- Thornton, K.W., Kennedy, R.H., Carroll, J.H., Walker, W.W., Gunkel, R.C., and Ashby, S. 1981. Reservoir sedimentation and water quality — an heuristic model. *In* Proceedings of the Symposium on Surface Water Impoundments, June 1980, Minneapolis, Minnesota. *Edited by* H.G. Stefan. American Society of Civil Engineers, New York. pp. 654–661.
- Thornton, K.W., Kimmel, B.L., and Payne, F.E. (*Editors*). 1990. Reservoir limnology: ecological perspectives. John Wiley & Sons, New York.
- Tundisi, J.G. 1993. Represas do Paraná Superior : limnologia e bases científicas para o gerenciamento. *In* Proceedings of the Conferencias de Limnologia La Plata, Instituto de Limnologia "Dr. R.A. Ringuelet", November 1992, Buenos Aires, Argentina. *Edited by* A. Boltovskoy and H.L. López. pp. 41–52.
- Tundisi, J.G., Matsumura-Tundisi, T., Henry, R., Rocha, O., and Hino, K. 1988. Comparação do estado trófico de 23 reservatórios do Estado de São Paulo: eutrofização e manejo. *In* Limnologia e manejo de represas. *Edited by* J.G. Tundisi. Série Monografias em Limnologia, Universidade de São Paulo, Escola de Engenharia de São Carlos, Cent. Recursos Hídricos Ecol. Aplicada, São Paulo, 1: 165–204.
- Wetzel, R.G. 1990. Reservoir ecosystems: conclusions and speculations. *In* Reservoir limnology: ecological perspectives. *Edited* by K.W. Thornton, B.L. Kimmel, and F.E. Payne. John Wiley & Sons, New York. pp. 227–246.
- Williams, J.D., Winemiller, K.O., Taphorn, D.C., and Balbas, L. 1998. Ecology and status of piscivores in Guri, an oligotrophic tropical Reservoir. N. Am. J. Fish. Manag. 18(2): 274–285.