

Migratory benthic fishes may induce regime shifts in a tropical floodplain pond

ROGER P. MORMUL*, SIDINEI M. THOMAZ[†], ANGELO A. AGOSTINHO[†],
CLAUDIA C. BONECKER[†] AND NESTOR MAZZEO[‡]

*Pós-graduação em Ecologia de Ambientes Aquáticos Continentais – PEA, Universidade Estadual de Maringá – UEM, Maringá – PR, Brazil

[†]Departamento de Biologia, Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura – Nupelia, Universidade Estadual de Maringá – UEM, Maringá – PR, Brazil

[‡]Departamento de Ecología & Evolución, CURE-Facultad de Ciencias, Universidad de La Republica, Maldonado, Uruguay

SUMMARY

1. Alternative states are a widely recorded phenomenon in shallow lakes, which may shift between turbid- and clear-water conditions. Here, we investigate whether such shifts in a tropical floodplain pond may be related to the effect of the flood pulse regime on the community structures of fish and macrophytes.

2. Using a long-term data set, we demonstrate how benthic fish migration together with colonisation by submerged plants affected the transition from a turbid to a macrophyte-dominated state in a floodplain pond without top-down control.

3. In our study, the turbid state occurred mostly during low water phases and was largely characterised by high values for the biomass of benthic fish, chlorophyll-*a* and total phosphorous.

4. During the period of rising water levels, the migration of benthic fish out of the pond occurs simultaneously with the establishment of submerged plants, while water turbidity decreases along with phytoplankton and nutrient concentrations, inducing a clear-water phase. However, when submerged plants are absent and fish migration is low, a transient state is generated.

5. We suggest that, in contrast to temperate ponds and shallow lakes, where the main driving mechanisms establishing alternative states are related to cascading effects via the food chain, in tropical ponds and shallow lakes it is resuspension of sediments by benthic fish that plays the most significant role in establishing alternative states. However, the effect of the flood pulse regime plays an important role in the temporal dynamics of fish community structure by controlling benthic fish migration.

Keywords: abrupt shifts, alternative states, *Egeria*, fish migration, flood pulse

Introduction

Shallow lakes are commonly characterised by alternative stable states, oscillating between a macrophyte-dominated state and a turbid state (dominated by a high abundance of phytoplankton and/or suspended matter concentration) (e.g. Scheffer *et al.*, 1993, 2001). Several studies examining alternative states have been based on correlations and models using long-term data obtained in the field (e.g. Brönmark *et al.*, 2010; Gelós *et al.*, 2010) or on

experiments carried out in mesocosms (e.g. Mazzeo *et al.*, 2010), while others have discussed the use of theoretical models (e.g. Scheffer & Jeppesen, 2007; Attayde *et al.*, 2010). These contrasting yet complementary approaches have provided fundamental insights and new hypotheses (e.g. Schooler *et al.*, 2011) that have supported the alternative states phenomenon as a convincing theory.

Most studies investigating regime shifts have been carried out in temperate regions, and few of these studies have included shifts occurring in river–floodplain systems

(e.g. Scheffer & Carpenter, 2003; Van Geest *et al.*, 2007), environments that are also rarely studied in the tropics (e.g. Loverde-Oliveira *et al.*, 2009). Independent of climatic region, water level fluctuation is an important factor that should be considered in river–floodplain ecosystems (Junk, Bayley & Sparks, 1989; Neiff, 1990; Thomaz, Bini & Bozelli, 2007). Different causes of regime shifts have been investigated, including storms (Schelske, Carrick & Aldridge, 1995), human activity (Scheffer, 1998), a combination of factors (Hargeby, Blindow & Hanson, 2004) and the presence of key species (Jeppesen *et al.*, 2007). Although temperate ecosystems have been more frequently investigated than those at other latitudes, new findings on regime shifts have also been reported for tropical (Loverde-Oliveira *et al.*, 2009) and subtropical lakes (Rodríguez-Gallego *et al.*, 2010), where the role of fish–macrophyte interactions seems to differ from that in temperate lakes (Meerhoff *et al.*, 2007). For example, the densities of small-bodied fish inside macrophyte stands are much higher in subtropical than in temperate waters (Jeppesen *et al.*, 2007), while submerged vegetation in subtropical lakes represents a poor refuge for large-bodied zooplankton, particularly cladocerans (Meerhoff *et al.*, 2003, 2006).

Despite the role of nutrient loading, many studies have illustrated the importance of multiple factors in initiating a shift (e.g. Scheffer *et al.*, 1993; Jones & Sayer, 2003; Liboriussen *et al.*, 2005; Hansson *et al.*, 2010). In general, the structure of the food web and nutrient availability are two of the crucial drivers of switches between alternative states. One example of a top-down cascade effect is the presence of piscivorous fish, which may induce a clear-water state because of their predation on planktivorous fish. Such predation leads to a reduction in predation pressure on zooplankton and a decrease in phytoplankton density, resulting in higher light availability throughout the water column (e.g. Scheffer *et al.*, 2001). On the other hand, the presence of benthic fish plays another critical role in the form of the bioturbation caused by the fish themselves. This disturbance results in sediment resuspension and nutrient release, allowing phytoplankton to flourish, which increases turbidity (e.g. Bergman *et al.*, 1999).

Some aquatic environments are strongly affected by external forces related to river basins. For example, river–floodplain systems are driven by hydrological regimes that affect their ecological functioning, biological attributes and physicochemical variables (Junk *et al.*, 1989; Neiff, 1990). In these systems, water level strongly influences limnological variables, with nutrients, chlorophyll and suspended material varying predictably in

response to the hydrological cycle (Camargo & Esteves, 1995; Lewis *et al.*, 2000). In this instance, shallow lakes within a river–floodplain system may shift between turbid- and clear-water states in response to flood pulses, as documented by Loverde-Oliveira *et al.* (2009) in the Pantanal wetlands of Brazil and by Hilt *et al.* (2011) via theoretical models for temperate lakes.

The Upper Paraná River floodplain is the last remaining undammed section of the Paraná River in Brazil (Agostinho *et al.*, 2004a), containing a variety of habitats (e.g. connected lakes, secondary channels, isolated lakes and wetland areas) and supporting a high diversity of organisms, particularly fish (Agostinho *et al.*, 2007). Some fish species are migratory and use the running water of the main channel and tributaries of the Paraná River for migration and spawning (Agostinho, Pelicice & Gomes, 2008a; Agostinho *et al.*, 2008b). The success of spawning depends on the presence of an overbank connection between the river and the surrounding lakes during migration, because floodplain lakes are used as nursery areas for the early phase of fish development (Agostinho *et al.*, 2004b). The most abundant migratory species are benthic and detritivorous (e.g. *Prochilodus lineatus* (Valenciennes); Agostinho *et al.*, 2004b), which supposedly affect water transparency by searching for and feeding on sediment.

In this study, we used data obtained from a shallow pond during a long-term ecological research (LTER) programme that was developed in the Upper Paraná floodplain to explore the temporal dynamics of shifts between turbid and clear states and to identify possible causal mechanisms. Taking into account the known effects of migratory fish and submerged macrophytes on the stability of regime shifts in shallow lakes (e.g. Brönmark *et al.*, 2010; Gelós *et al.*, 2010; Rodríguez-Gallego *et al.*, 2010), we used the biomass of benthic fish, primarily represented by *P. lineatus*, and the degree of colonisation of the submerged macrophyte *Egeria densa* Planc to explain long-term changes (*c.* 6 years) in pond water features. Although based on observational data, our study makes a useful contribution to the alternative states theory by providing long-term measurements and initial hypotheses regarding regime shifts in a tropical floodplain pond.

Methods

Study area

The Upper Paraná River floodplain is a complex mosaic mostly made up of wetlands, but also includes forest fragments, riparian vegetation, marsh forests, shrubby

vegetation and grasslands. Aside from large river channels, the floodplain also contains shallow permanent lakes, temporary lakes, secondary channels and more than 100 islands, as well as sandy and swampy beaches (Mendonça, Lopes & Anjos, 2009).

Osmar Pond ($22^{\circ}46'27.53''\text{S}$ and $53^{\circ}19'57.95''\text{W}$; Fig. 1) is a very small isolated lake located c. 120 m from the Paraná River channel. It is sixty metres long and 15 m wide on average during the low water phase, whereas in high water periods it reaches an average area of 0.15 ha, with depths varying from 0.6 m (low water period) to 4.5 m (high water period) during the study period. The pond is surrounded by well-preserved, high and dense riparian vegetation on a predominantly sandy soil (developed on a sandstone substrate). The overbank connection between the river and the pond occurs primarily during high water periods and forms when the river reaches a water level of 3 m; however, exchanges between the river and the pond through the hyporheic corridor may also occur when the river's water level is <3 m.

The floodplain's seasonal water level fluctuations are affected primarily by the pluviometric dynamics of the basin and by the operation of dams located upstream of the plain. High water levels predominate between November and March (rainy seasons – spring and summer), with low water levels occurring between April

and October (dry seasons – autumn and winter). Long-term data indicate that water levels fluctuate, on average, 2.5 m per year with a maximum amplitude of c. 7.5 m (Agostinho *et al.*, 2008b).

Sample regimes

Sampling was carried out at 3 month intervals from March 2005 to December 2010. The water level of the Paraná River was recorded daily at a station located 12 km upstream from the pond. For this variable, we used the mean of the recorded water levels for the 7 days preceding the sampling day. We used this procedure because limnological parameters in the Paraná floodplain lakes are most strongly correlated with the Paraná River water level at a time lag of 7 days (Thomaz *et al.*, 2004). Although pond depth was also measured, we preferred to use river water level because (i) this is a more meaningful variable relating to flood pulses, (ii) it indicates the approximate level at which the pond connects to the river and (iii) both river water level and pond depth were highly and significantly correlated ($r = 0.97$, $P < 0.001$). Turbidity was measured (via a turbidity meter; LaMotte, Chestertown, MD, U.S.A) below the surface in the pelagic zone. In the same location, water samples were collected for the analysis of chlorophyll-*a* and nutrient concentra-

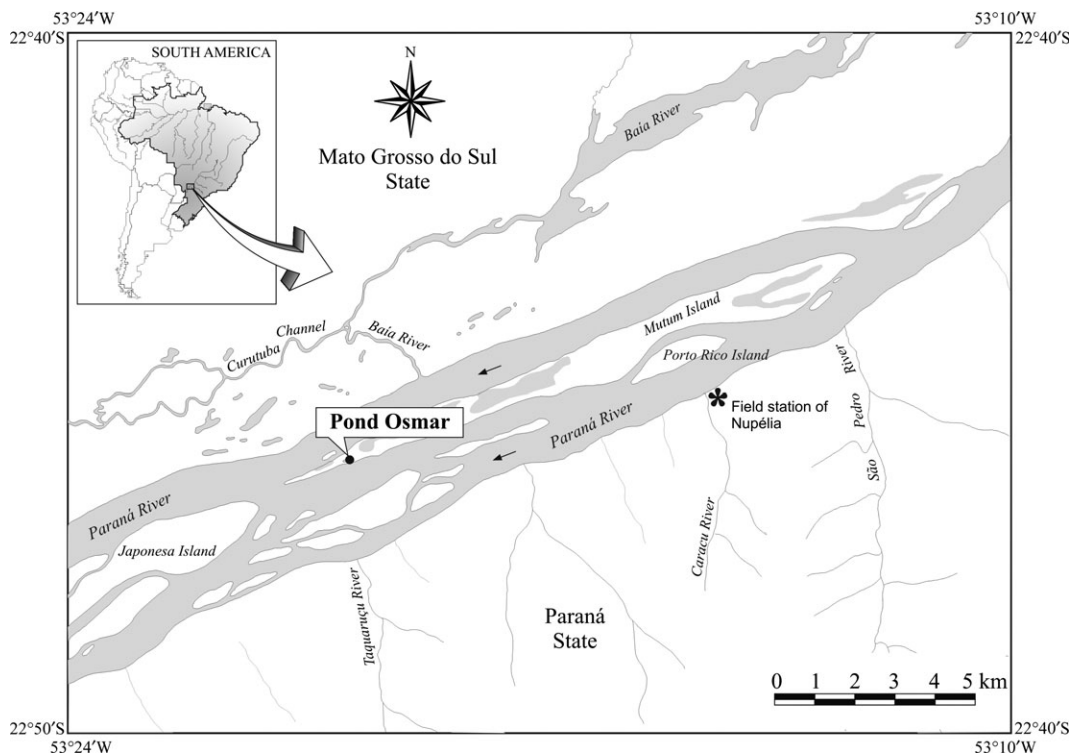


Fig. 1 Map of the stretch of the Upper Paraná River floodplain containing Osmar Pond.

tions. Although wind could be an important variable, we did not measure this factor because it changes markedly over short periods and wind measured at a particular time would be of little relevance, and the shoreline is surrounded by high and dense vegetation that reduces the effect of wind on the pond.

Water samples were filtered using Whatman™ GF 52-C membranes (GE Healthcare Latin America, São Paulo, SP, Brazil) to quantify chlorophyll-*a*. The pigment was extracted with acetone, and the samples were read in a spectrophotometer according to the method of Golterman, Clymo & Ohmstad (1978). Total nitrogen was analysed via the persulphate method (Bergamin, Reis & Zagatto, 1978) and determined in a spectrophotometer in the presence of cadmium, using a flow-injection system (Giné *et al.*, 1980). Total phosphorus (TP) was measured according to Golterman *et al.* (1978).

Zooplankton, fish and macrophyte communities were also sampled at the same location. Zooplankton samples were obtained below the surface in the pelagic zone using a motorised pump and a plankton net (68 µm), with 1000 L of water filtered per sample. Samples were preserved in a 4% formaldehyde solution buffered with calcium carbonate (Lansac-Tôha *et al.*, 2009). In the laboratory, samples were analysed under the microscope to count (individuals m⁻³) and identify organisms to the lowest taxonomic level possible. Zooplankton community structure was analysed in terms of functional groups: small-sized filter-feeders (rotifers and nauplii), medium-sized filter-feeders (cladocerans and calanoids) and omnivores–carnivores (cyclopoids).

The fish community was always sampled at the same site with a seine net 20 m long, 1.5 m in height and with a 0.5 cm mesh. The seine started in open water towards to the shore. The entire water column was always sampled, taking into account the height of the seine net to start the seine. The biomass of each fish species (g m⁻²) was estimated based on the seined area. Employing the trophic guild classification provided by Hahn, Fugi & Andrian (2004), we separated fish species into six guilds: (i) herbivorous (ii) detritivorous (iii) invertivorous (iv) insectivorous (v) piscivorous and (vi) omnivorous (Table 1). In addition, fish species were divided based on three habitat preferences: (i) pelagic (ii) benthic and (iii) pelagic–benthic (Table 1). Finally, macrophyte community samples were taken using a rake held from a boat travelling at a constant velocity, traversing the entire pond to record submerged species. The macrophyte cover area was estimated using a square (0.5 m²) positioned at every metre along two transects crossing the pond.

Table 1 Species list of fish and functional classifications (trophic guild; habitat preference) considered in analyses

Trophic guild	Habitat		
	P	B	P-B
Herbivorous			
* <i>Hyphessobrycon eques</i> (Steindachner)			X
* <i>Metynnis lippincottianus</i> (Cope)	X		
Detritivorous			
* <i>Cyphocharax modestus</i> (Fernandez-Yépez)		X	
<i>Loricariichthys platymetopon</i> (Isbrucker and Nijssen)		X	
<i>Prochilodus lineatus</i> (Valenciennes)		X	
<i>Pterygoplichthys ambrosettii</i> (Holmberg)		X	
<i>Steindachnerina brevipinna</i> (Eigenmann and Eigenmann)		X	
<i>Steindachnerina insculpta</i> (Fernandéz-Yepe)		X	
Invertivorous			
* <i>Aphyocharax anisitsi</i> (Eigenmann and Kennedy)			X
* <i>Aphyocharax dentatus</i> (Eigenmann and Kennedy)			X
* <i>Apistogramma commbrae</i> (Regan)			X
* <i>Hoplosternum littorale</i> (Hancock)		X	
* <i>Pamphorichthys</i> sp			X
<i>Satanoperca pappaterra</i> (Heckel)		X	
Insectivorous			
* <i>Astyanax altiparanae</i> (Garutti and Britski)	X		
* <i>Bryconamericus stramineus</i> (Eigenmann)	X		
* <i>Characidium zebra</i> (Eigenmann)		X	
<i>Crenicichla britskii</i> (Kullander)		X	
* <i>Hyphessobrycon</i> sp			X
* <i>Moenkhausia forestii</i> (Benine, Mariguela and Oliveira)	X		
* <i>Moenkhausia intermedia</i> (Eigenmann)	X		
* <i>Odonthostilbe</i> sp			X
Piscivorous			
<i>Acestrorhynchus lacustris</i> (Reinhardt)		X	
* <i>Cichla kelberi</i> (Kullander and Ferreira)		X	
<i>Hoplerythrinus unitaeniatus</i> (Spix and Agassiz)		X	
<i>Hoplias</i> sp		X	
<i>Pseudoplatystoma corruscans</i> (Spix and Agassiz)			X
* <i>Roebooides descavadensis</i> (Fowler)		X	
<i>Serrasalmus marginatus</i> (Valenciennes)		X	
Omnivorous			
* <i>Astronotus crassipinnis</i> (Heckel)			X
* <i>Cichlasoma paranaense</i> (Kullander)		X	
<i>Leporinus obtusidens</i> (Valenciennes)			X
* <i>Psellogrammus kennedyi</i> (Eigenmann)			X
* <i>Serrapinnus notomelas</i> (Eigenmann)	X		

P, pelagic; B, benthic; P-B, pelagic-benthic.

*Typical lake fish species.

Data analysis

The relationships between all variables were verified using a Spearman's rank correlation matrix with individually based data. Because macrophytes were present only from June to December 2009 (see Results), it was not possible to apply this test to plant coverage. A model selection approach using the Spatial Analysis in Macroecology – SAM software (Rangel, Diniz-Filho & Bini, 2010) – was applied with the aim of selecting the

most parsimonious linear model based on the Akaike information criterion (AIC; Burnham & Anderson, 2002), with turbidity and chlorophyll-*a* as the response variables. Turbidity and chlorophyll-*a* were chosen because they are generally considered to be the most important variables when assessing different stable states, as well as shifts between those states. Finally, Spearman's rank correlation was used to assess whether the data acquired on the first sampling date were significantly correlated with later measurements (a time series of 23 samplings). For that, we used a matrix in which the rows contained all of the variables exhibiting significant relationships in Table 2 (see Results) and the columns contained sampling dates. Thus, the first sampling date was compared on a pairwise basis with the second, third and fourth sampling dates and so on, up to the 23rd sampling date. According to this method, the persistence of a state produces significant correlation between samples, whereas shifts are indicated by non-significant correlations. This procedure was carried out twice, with and without the inclusion of macrophyte cover data, to remove the effect of the low number of macrophyte records. To determine which fish species are typically lake fish species (see Table 1), we analysed the proportion of occurrences of each species between lakes and rivers in the Paraná River floodplain, considering typical lake fish species to be those with at least 90% of their reported occurrences in lakes.

Results

Over the course of the long-term monitoring programme (carried out beginning in 2005), wide variations in all limnological factors were recorded. However, three main phases could be identified as follows:

Phase (1) was characterised by low values of chlorophyll-*a*, TP and turbidity (Fig. 2A,B). A 6-month peak in small-sized filter-feeders zooplankton was recorded (Fig. 2C), and in general, piscivorous and insectivorous fish dominated (Fig. 2D) and there was low biomass or absence of benthic fish (Fig. 2E). This pattern was observed from March 2005 to June 2005, November 2005 to March 2007, February 2008 to September 2008 and December 2009 to December 2010. These periods usually occurred when the water level was between 2.5 and 3.0 m (i.e. prior to the formation of an overbank connection) or above 3.0 m (when overbank connections occur).

Phase (2) was characterised by peak values of chlorophyll-*a*, TP and turbidity (Fig. 2A,B), the dominance of small-sized filter-feeders and omnivores–carnivores zooplankton (Fig. 2C), as well as peaks in the biomass of

Table 2 Values of Spearman's rank correlation for significant results ($P < 0.05$)

Variables	<i>P</i>
Water level × Turbidity	−0.53
Water level × Chlorophyll	−0.73
Water level × Total phosphorus	−0.68
Water level × Herbivorous	−0.48
Water level × Detritivorous	−0.58
Water level × Benthic	−0.59
Turbidity × Chlorophyll	0.51
Turbidity × Total phosphorus	0.74
Turbidity × Herbivorous	0.43
Turbidity × Detritivorous	0.42
Turbidity × Benthic	0.45
Chlorophyll × Total phosphorus	0.70
Chlorophyll × Herbivorous	0.64
Chlorophyll × Detritivorous	0.72
Chlorophyll × Benthic	0.76
Chlorophyll × Pelagic-benthic	0.61
Total phosphorus × Herbivorous	0.40
Total phosphorus × Detritivorous	0.59
Total phosphorus × Benthic	0.66
Pelagic × Insectivorous	0.55
Pelagic × Piscivorous	0.77
Pelagic × Omnivorous	0.62
Benthic × Herbivorous	0.73
Pelagic × Detritivorous	0.99
Pelagic-benthic × Invertivorous	0.42
Pelagic-benthic × Omnivorous	0.82
Pelagic-benthic × Detritivorous	0.63

piscivorous, detritivorous and invertivorous fish (Fig. 2D), and pelagic, benthic and pelagic–benthic fish (Fig. 2E). This pattern was observed from June 2005 to November 2005, March 2007 to February 2008 and September 2008 to June 2009. These phases occurred when water was receding and followed the highest flood episode, when the pond was at its shallowest state (river water level in general lower than 2.5 m).

Phase (3) was observed from June 2009 to December 2009. It occurred in rising water, when the water level was above 3.0 m, benthic, insectivorous and omnivorous fish declined towards a complete absence in December, while macrophytes covered *c.* 28% of the pond surface (Fig. 2A) and the lowest values for turbidity and chlorophyll-*a* were recorded (Fig. 2B); small-sized filter-feeders zooplankton were present at very low densities (Fig. 2C).

These phases were also suggested by the significant relationships between several variables (Table 2). These correlations indicate that turbidity, chlorophyll-*a*, TP and benthic fish biomass increased with decreasing water levels, while chlorophyll-*a*, TP and benthic fish biomass increased together with turbidity, but seemed to decrease in the presence of submerged vegetation (Fig. 2A,B). In addition, chlorophyll-*a* increased with TP and benthic

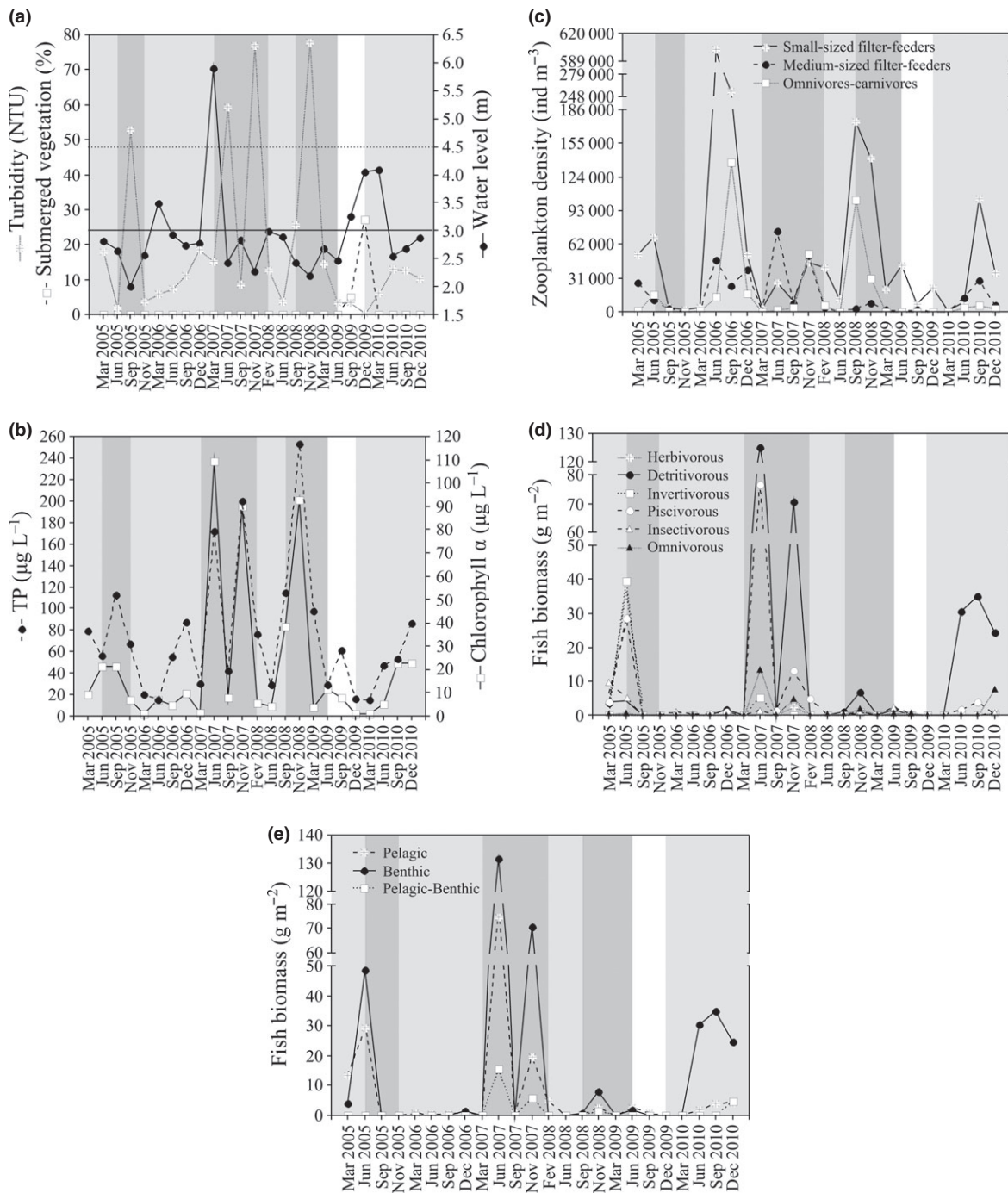


Fig. 2 Temporal trends in observed water levels for the main river channel, turbidity and submerged vegetation (a), where the horizontal full line represents the approximate starting point for the overbank connection between the pond and the river, and the horizontal dashed line indicates the approximate point at which the pond becomes a flowing system; total phosphorus and chlorophyll-*a* (b); density of small and medium-sized filter-feeder and omnivore-carnivore zooplankton (c); fish biomass for each trophic guild (d); and fish biomass for each habitat preference (e). Submerged vegetation is given as a percentage of the area of the whole pond, while a light gray column indicates a transient state, a dark gray column a turbid state and a white column a macrophyte-dominated state.

fish, with TP concentration also increasing with benthic fish biomass.

In contrast, no significant relationships were found between the densities of piscivorous and potentially

planktivorous fish (insectivorous, invertivorous and omnivorous; Spearman correlation, $P > 0.05$). In addition, the correlations of small-sized filter-feeders, medium-sized filter-feeders and omnivores-carnivores zooplank-

ton with potentially planktivorous fish biomass and chlorophyll-*a* concentration were not significant (Spearman correlation, $P > 0.05$).

Although turbidity was significantly related to several variables (see Table 2), model selection indicated that benthic fish (g m^{-2}) and TP ($\mu\text{g L}^{-1}$) were the most important variables for predicting values of turbidity in Osmar Pond ($R^2 = 0.87$, AICc = 180.68, AICc wi = 0.218),

$$\text{Turbidity} = -6.968 + (0.065 * \text{Benthic}) + (0.333 * \text{TP})$$

Benthic fish and TP were also the most important predictors of chlorophyll according to the AIC ($R^2 = 0.92$, AICc = 181.57, AICc wi = 0.232),

$$\text{Chlorophyll} = -11.685 + (0.425 * \text{Benthic}) + (0.35 * \text{TP})$$

Thus, benthic fish and TP were the most important variables, because of their appearance in the most parsimonious models explaining both turbidity and chlorophyll-*a*.

Finally, significant correlations were observed between the group of variables recorded for the first sampling date and for the following samplings, up until June 2009 (Spearman correlation, $0.79 < r < 0.96$, $P < 0.05$; Fig. 3). However, when the presence of *E. densa* was observed in September and December 2009, the correlation between those sampling dates and the first sampling became non-significant (Spearman correlation, $P > 0.05$), providing evidence that the limnological features of the pond for these 2 months differed from the other dates. The strongest difference occurred in December, when a shift towards a clear-water, macrophyte-dominated state occurred, as

indicated by some of the lowest values of turbidity, chlorophyll-*a* and TP concentrations (see Fig. 2A,B). In contrast, the data taken on the four sampling dates of 2010 were once again significantly correlated with the data obtained on the first sampling date (Spearman correlation, $0.62 < r < 0.88$, $P < 0.05$; Fig. 3), indicating that the pond shifted back to a phase similar to the one found before *E. densa* colonisation. The correlation analysis without the inclusion of macrophyte cover data confirmed that the sample collected in December 2009 was not significantly correlated with those of the first sampling (Spearman correlation, $r = -0.03$, $P > 0.05$; Fig. 3), reinforcing our results.

Discussion

Our findings from *c.* 6 years of measurement of turbidity and chlorophyll-*a* levels in a tropical floodplain pond illustrate the possible occurrence of three water states (Fig. 4). The turbid state occurred when the pond was at its shallowest phase and was characterised by high biomass of benthic fish and high values of TP, turbidity and chlorophyll-*a*, while the macrophyte-dominated state occurred at the high water phase and exhibited the lowest values of TP, turbidity and chlorophyll-*a*. Despite the fact that the transient state does not appear to have been clearly detected by the Spearman's analysis, suggesting greater similarity with the turbid state, a transient state may be observed during periods of intermediate water levels. The transient state was characterised by absence of submerged macrophytes, low benthic fish biomass, intermediate values of TP, turbidity and chlorophyll-*a* relative to the other two states, as well as high zooplankton densities, primarily small-sized filter-feeders. The indicators of alternative states in shallow lakes chosen here (turbidity and chlorophyll-*a*) correlated positively with TP and benthic fish biomass. These explanatory variables are also the only ones appearing in the 'best' models according to the Akaike criterion. It is also worth noting that the macrophyte-dominated state occurred only for *c.* 6 months (in a total of *c.* 6 years of analysis), when benthic fish were absent, but benthic fish were also absent in a macrophyte-free period, potentially indicating that factors other than absence of fish could also be important for triggering macrophyte growth in the system.

Given the congruence of these different analyses, we can speculate on the causal mechanisms behind the shifts observed in this pond. However, we caution that such inferences should be considered as hypotheses in view of the observational nature of our data. We suggest that an

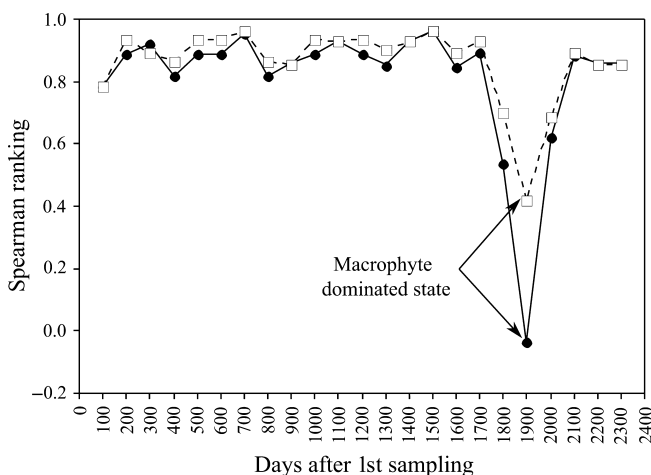


Fig. 3 Values of Spearman's rank correlation of the first sampling date (March 2005) against other sampling dates. The dashed line represents the correlation excluding macrophyte data.

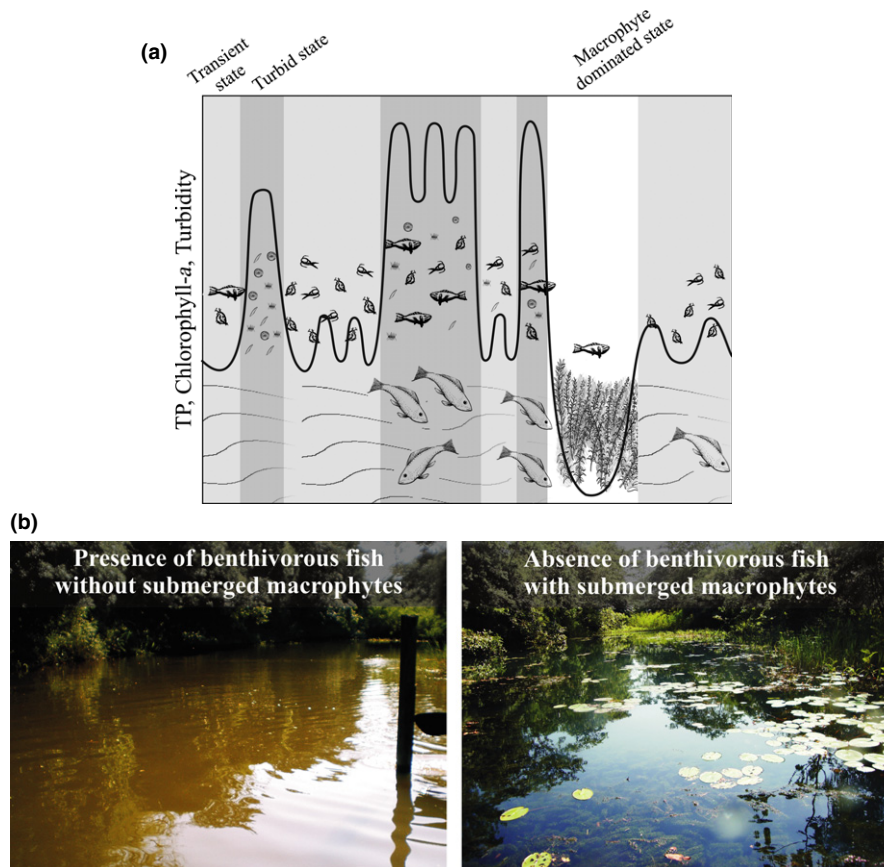


Fig. 4 Conceptual model illustrating the three states recorded at Osmar Pond (a), with photos of the turbid and macrophyte-dominated states (b). The full line indicates trends for total phosphorus, chlorophyll-*a* and turbidity.

increase in benthic fish biomass enhanced sediment resuspension and nutrient release, leading to high turbidity and chlorophyll-*a* concentrations (turbid state; e.g. June 2007, November 2007 and 2008), which can be enhanced by the lack of flushing or mixing with clear water from the river. Although P release from sediment could partially explain these results, we reject this possibility because the Paraná floodplain's shallow lakes and ponds are highly oxygenated during low water periods (Thomaz *et al.*, 2004; Lemke *et al.*, 2010). In addition, owing to the height and density of vegetation sheltering the shoreline of the pond, it is improbable that wind had significant effects on sediment resuspension at high water level. However, a turbid state may also be reached when the pond is extremely shallow (e.g. September 2005). In this case, sediment resuspension by wind and animals is one possible explanation (Thomaz *et al.*, 2004). The transient state still occurred below the water level at which overbank connection occurs (*c.* 2.5–3.0 m) and could be associated with exchanges between pond and river water through the hyporheic corridor, which may dilute pond water (Thomaz *et al.*, 2007) and reduce the effect of fish on

turbidity. When macrophytes were present, nutrients and turbidity were reduced considerably and a true clear-water state was attained. Thus, our results illustrate the possible effect of fish community structure on the turbidity of a tropical floodplain pond, a mechanism similar to that proposed by Bergman *et al.* (1999) for temperate lakes.

In shallow lakes, several mechanisms are involved in initiating the shift from a turbid to a clear-water state (Scheffer *et al.*, 1993, 2001). The main factor driving the phenomenon seems to be the interaction between submerged macrophytes and turbidity (Scheffer *et al.*, 1993). Aside from competing with phytoplankton for resources (light and nutrients), macrophytes promote the sedimentation of microalgae, reduce the effect of resuspension caused by wind and fish activity and provide refuges for zooplankton and young piscivorous fish (Gulati & Donk, 2002). Our results are possibly related to these mechanisms because although correlations between fish, zooplankton and phytoplankton were non-significant, we found reductions in phytoplankton and turbidity in the presence of submerged macrophytes. Another important

factor initiating shifts between states, mainly in temperate lakes, is thought to be the top-down control provided by potentially piscivorous fish in helping to increase the number of medium-sized filter-feeders, which in turn leads to a reduction in phytoplankton biomass and enhancement of water transparency (Scheffer, 1990). However, the water states in Osmar Pond presented in this study differ from this previous description in two important respects: first, top-down control by piscivorous fish seems to be less important in Osmar Pond than in temperate lakes because medium-sized filter-feeders occurred in very low densities during periods when macrophytes dominated (see Fig. 2A,C); second, we identified a transient state accompanied by an absence of macrophytes, low abundance of benthic fish and dominance of the zooplankton by rotifers and nauplii.

The role of water level oscillation (linked to water exchange between the lake and the adjacent river) in the recurrence of alternative states has been studied in a tropical floodplain lake (e.g. Loverde-Oliveira *et al.*, 2009). However, the role of the flood pulse on fish community structure remained unknown in this lake. In the same way, temperate lakes connected with clear-water rivers are hypothesised to shift from a turbid to a clear-water state because of the dilution effects of the clear-water of the river entering the lake, but such a shift occurs in combination with the growing season of submerged macrophytes and a strong flushing rate (Hilt *et al.*, 2011).

In contrast with the results of Loverde-Oliveira *et al.* (2009) and Hilt *et al.* (2011), the influence of water level on turbidity in Osmar Pond is rather more indirect, although water in the main river is highly transparent because of the retention of solids and nutrients by the cascade of dams located upstream. For most of the year, the pond is not connected to the main river because of an elevated natural levee, and in our study the pond became a flowing system only in March 2007. However, when an overbank connection with the river forms, young-of-the-year benthic fish enter the pond and immature adult benthic fish leave the pond (Agostinho *et al.*, 2008a). Thus, in years of high recruitment, increased numbers of young-of-the-year benthic fish make the pond water turbid, especially when the pond is shallow. Nevertheless, the connection provided by floods also enables significant migration by immature adult benthic fish to the river, reducing bioturbation in the pond and decreasing water turbidity. In addition, floods also transport the propagules of submerged plants (as already suggested for the Pantanal wetlands by Loverde-Oliveira *et al.*, 2009 and in the Paraná River by Thomaz *et al.*, 2009). The colonisation of Osmar Pond by submerged plants may have accelerated

the shift from a turbid to a clear-water state observed at the end of 2009. Thus, although obtained in a single pond, our data suggest that for tropical floodplain ponds or tropical floodplain shallow lakes, the timing of fish migration is just as important a determinant of the establishment of submerged macrophytes as it is for temperate lakes (e.g. Brönmark *et al.*, 2010). The occurrence of a clear-water, macrophyte-dominated state in these lakes may therefore depend on hydrological connectivity.

The mechanism that we hypothesise to occur in Osmar Pond is similar to that described by Bergman *et al.* (1999), in which benthic fishes cause bioturbation and sediment resuspension, increasing turbidity. At the same time, nutrients were released from the sediment through fish-induced bioturbation, allowing phytoplankton to flourish and dominate the pond in its turbid state. In contrast, the establishment of submerged vegetation was most likely favoured by the reduction in suspended material and disturbances caused by declining fish numbers. Subsequent macrophyte growth, eventually covering c. 28% of the whole pond surface, stabilised the water column and inhibited wind and fish-induced sediment resuspension, which could help to maintain a clear-water state. The absence of significant correlations between the data obtained from the first sampling date and those obtained in 2009 only reinforces the importance of the reduction in benthic fish numbers and the establishment of the submerged macrophytes.

In our results, we observed low zooplankton densities during periods of macrophyte dominance. Additionally, potentially planktivorous fish were also rare during the same period; the low abundance of zooplankton at Osmar Pond is therefore not associated with predation by fish, but may instead be a result of dilution caused by the influx of water. In this sense, our results do not reinforce those from other subtropical lakes that indicate macrophytes represent poor refuge against fish predation (Meerhoff *et al.*, 2003, 2006).

The establishment of a clear-water state at Osmar Pond, dominated in the short term by *E. densa*, was probably made possible due to the extremely high growth rate of this species (Yarrow *et al.*, 2009). Subsequent increases in turbidity (in part derived from benthic activity) and water depth resulted in *E. densa*'s collapse and shifted the pond towards a turbid state. We also suggest that, although a reduction in benthic fish and increase in filter-feeders zooplankton densities may decrease turbidity, a shift from a turbid to a clear-water state seems to be facilitated by the presence of submerged macrophytes. However, the diluting effect of the flood pulse and accompanying arrival of other

species owing to increased hydrological connectivity during floods may change the dynamic of the pond in the long term. In this way, the pond would pass from a pattern similar to that described by Bergman *et al.* (1999), with shifts driven by benthic fish, to that described by Loverde-Oliveira *et al.* (2009), with shifts driven by the hydrological regime.

In summary, although resuspension of sediments by benthic fish has been reported in temperate regions, the main driving mechanisms in establishing patterns of turbidity in temperate ponds and shallow lakes is fish community structure in relation to cascading effects via the food chain. Here, we suggest that the main driving mechanisms in establishing patterns of turbidity in tropical ponds and shallow lakes are also related to fish community structure. However, in tropical regions, resuspension of sediments by benthic fish may play the most significant role in establishing these patterns, even in floodplains for which hydrological regimes are generally considered to be the main driving force behind changes in limnological and biological attributes.

Acknowledgments

RPM thanks the Brazilian Council for Scientific and Technological Development (CNPq) for providing his PhD scholarship; Dr. Christer Brönmark and Dr. Lars-Anders Hansson for fundamental insights during the writing of the manuscript draft, and Dr. Francisco de Assis Esteves and Dr. Reinaldo Luiz Bozelli for critical reading of the final version. SMT, AAA and CCB are researchers in Scientific Productivity at the CNPq and acknowledge this agency for long-term provision of funds. This research was carried out as part of the Long Term Ecological Research Project (LTER) funded by the CNPq and the Ministry of Science and Technology.

References

- Agostinho A.A., Gomes L.C., Pelicice F.M., Souza-Filho E.E. & Tomanik E.A. (2008b) Application of the ecohydrological concept for sustainable development of tropical floodplains: the case of the upper Parana River basin. *Ecology and Hydrobiology*, **8**, 205–223.
- Agostinho A.A., Gomes L.C., Verissimo S. & Okada E.K. (2004b) Flood regime, dam regulation and fish in the Upper Parana River: effects on assemblage attributes, reproduction and recruitment. *Reviews in Fish Biology and Fisheries*, **14**, 11–19.
- Agostinho A.A., Pelicice F.M. & Gomes L.C. (2008a) Dams and the fish fauna of the neotropical region: impacts and management related to diversity and fisheries. *Brazilian Journal of Biology*, **68**, 1119–1133.
- Agostinho A.A., Pelicice F.M., Petry A.C., Gomes L.C. & Julio H.E. (2007) Fish diversity in the upper Parana River basin: habitats, fisheries, management and conservation. *Aquatic Ecosystem Health & Management*, **10**, 174–186.
- Agostinho A.A., Rodrigues L., Gomes L.C., Thomaz S.M. & Miranda L.E. (2004a) *Structure and Functioning of the Paraná River and its Floodplain*. Eduem, Maringá, Paraná, Brazil.
- Attayde J.L., Van Nes E.H., Araujo A.I.L., Corso G. & Scheffer M. (2010) Omnivory by planktivores stabilizes plankton dynamics, but may either promote or reduce algal biomass. *Ecosystems*, **13**, 410–420.
- Bergamin H., Reis B.F. & Zagatto E.A.G. (1978) A new device for improving sensitivity and stabilization in flow injection analysis. *Analytica Chimica Acta*, **97**, 427–431.
- Bergman E., Hansson L.-A., Persson A., Strand J., Romare P., Enell M. *et al.* (1999) Synthesis of theoretical and empirical experiences from nutrient and cyprinid reductions in Lake Ringsjön. *Hydrobiologia*, **404**, 145–156.
- Brönmark C., Brodersen J., Chapman B.B., Nicolle A., Nilsson P.A., Skov C. *et al.* (2010) Regime shifts in shallow lakes: the importance of seasonal migration. *Hydrobiologia*, **646**, 91–100.
- Burnham K.P. & Anderson D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer-Verlag, New York.
- Camargo A.F.M. & Esteves F.A. (1995) Influence of water-level variation on fertilization of an oxbow lake of Rio Mogi-Guaçu, State of Sao Paulo, Brazil. *Hydrobiologia*, **299**, 185–193.
- Gelós M., Teixeira-de-Mello F., Goyenola G., Iglesias C., Fosalba C., Garcia-Rodriguez F. *et al.* (2010) Seasonal and diel changes in fish activity and potential cascading effects in subtropical shallow lakes with different water transparency. *Hydrobiologia*, **646**, 173–185.
- Giné M.F., Bargamin F.H., Zagatto E.A.G. & Reis B.F. (1980) Simultaneous determination of nitrate and nitrite by flow injection analysis. *Analytica Chimica Acta*, **114**, 191–197.
- Golterman H.L., Clymo R.S. & Ohmstad M.A.M. (1978) *Methods for Physical and Chemical Analysis of Freshwater*. Blackwell Scientific, Oxford.
- Gulati R.D. & Donk E. (2002) Lakes in the Netherlands, their origin, eutrophication and restoration: state-of-the-art review. *Hydrobiologia*, **478**, 73–106.
- Hahn N.S., Fugi R. & Andrian I.F. (2004) Trophic ecology of the fish assemblages. In: *The Upper Paraná River and its Floodplain: Physical Aspects, Ecology and Conservation* (Eds S.M. Thomaz, A.A. Agostinho & N.S. Hahn), pp. 247–269. Backhuys Publishers, Leiden.
- Hansson L.-A., Nicolle A., Brönmark C., Hargeby A., Lindstrom A. & Andersson G. (2010) Waterfowl, macrophytes, and the clear water state of shallow lakes. *Hydrobiologia*, **646**, 101–109.
- Hargeby A., Blindow I. & Hanson L.-A. (2004) Shifts between clear and turbid states in a shallow lakes: multi-causal

- stress from climate, nutrients and biotic interactions. *Archiv für Hydrobiologie*, **161**, 433–454.
- Hilt S., Kohler J., Kozerski H.-P., van Nes E.H. & Scheffer M. (2011) Abrupt regime shifts in space and time along rivers and connected lake systems. *Oikos*, **120**, 766–775.
- Jeppesen E., Sondergaard M., Pedersen A.R., Jurgens K., Strzelczak A., Lauridsen T.L. *et al.* (2007) Salinity induced regime shift in shallow brackish lagoons. *Ecosystems*, **10**, 48–58.
- Jones J.I. & Sayer C.D. (2003) Does the fish-invertebrate-periphyton cascade precipitate plant loss in shallow lakes? *Ecology*, **84**, 2155–2167.
- Junk W.J., Bayley P.B. & Sparks R.E. (1989) The flood pulse concept in river-floodplain systems. *Canadian Journal of Fisheries and Aquatic Sciences*, **106**, 110–127.
- Lansac-Tôha F.A., Bonecker C.C., Velho L.F.M., Simões N.R., Dias J.D., Alves G.M. *et al.* (2009) Biodiversity of zooplankton communities in the Upper Parana River floodplain: interannual variation from long-term studies. *Brazilian Journal of Biology*, **69**, 539–549.
- Lemke M.J., Pagioro T.A., Lemke A.M. & Thomaz S.M. (2010) Diel variation related to thermal mixing in a subtropical and in a north-temperate shallow floodplain lake. *Journal of Freshwater Ecology*, **25**, 373–383.
- Lewis W.M. Jr, Hamilton S.K., Lasi M.A., Rodriguez M. & Saunders J.F. III (2000) Ecological determinism on the Orinoco floodplain. *BioScience*, **50**, 681–692.
- Liboriussen L., Jeppesen E., Bramm M.E. & Lassen M.F. (2005) Periphyton–macroinvertebrate interactions in light and fish manipulated enclosures in a clear and a turbid shallow lake. *Aquatic Ecology*, **39**, 23–39.
- Loverde-Oliveira S.M., Huszar V.L.M., Mazzeo N. & Scheffer M. (2009) Hydrology-driven regime shifts in a shallow tropical lake. *Ecosystems*, **12**, 807–819.
- Mazzeo N., Iglesias C., Teixeira-de-Mello F., Borthagaray A., Fosalba C., Ballabio R. *et al.* (2010) Trophic cascade effects of *Hoplias malabaricus* (Characiformes, Erythrinidae) in subtropical lakes food webs: a mesocosm approach. *Hydrobiologia*, **644**, 325–335.
- Meerhoff M., Fosalba C., Bruzzone C., Mazzeo N., Noordoven W. & Jeppesen E. (2006) An experimental study of habitat choice by *Daphnia*: plants signal danger more than refuge in subtropical lakes. *Freshwater Biology*, **51**, 1320–1330.
- Meerhoff M., Iglesias C., Teixeira-de-Mello F., Clemente J.M., Jensen E., Lauridsen T.L. *et al.* (2007) Effects of habitat complexity on community structure and predator avoidance behaviour of littoral zooplankton in temperate versus subtropical shallow lakes. *Freshwater Biology*, **52**, 1009–1021.
- Meerhoff M., Mazzeo N., Moss B. & Gallego-Rodriguez L. (2003) The structuring role of free-floating versus submerged plants in a subtropical shallow lake. *Aquatic Ecology*, **37**, 377–391.
- Mendonça L.B., Lopes E.V. & Anjos L. (2009) On the possible extinction of bird species in the Upper Parana River floodplain, Brazil. *Brazilian Journal of Biology*, **69**, 747–755.
- Neiff J.J. (1990) Ideas para la interpretacion ecologica del Parana. *Interciencia*, **15**, 424–441.
- Rangel T.F., Diniz-Filho J.A.F. & Bini L.M. (2010) SAM: a comprehensive application for Spatial Analysis in Macroecology. *Ecography*, **33**, 46–50.
- Rodríguez-Gallego L., Meerhoff E., Clemente J.M. & Conde D. (2010) Can ephemeral proliferations of submerged macrophytes influence zoobenthos and water quality in coastal lagoons? *Hydrobiologia*, **646**, 253–269.
- Scheffer M. (1990) Multiplicity of stable states in freshwater systems. *Hydrobiologia*, **200/201**, 475–486.
- Scheffer M. (1998) *Ecology of Shallow Lakes*, 1st edn. Chapman and Hall, London.
- Scheffer M. & Carpenter S.R. (2003) Catastrophic shifts in ecosystems: linking theory to observations. *Trends in Ecology & Evolution*, **18**, 648–656.
- Scheffer M., Carpenter S.R., Foley J.A., Folke C. & Walker B. (2001) Catastrophic shifts in ecosystems. *Nature*, **413**, 591–596.
- Scheffer M., Hosper S.H., Meijer M.-L., Moss B. & Jeppesen E. (1993) Alternative equilibria in shallow lakes. *Trends in Ecology & Evolution*, **8**, 275–279.
- Scheffer M. & Jeppesen E. (2007) Regime shifts in shallow lakes. *Ecosystems*, **10**, 1–3.
- Schelske C.L., Carrick H.J. & Aldridge F.J. (1995) Can wind-induced resuspension of meroplankton affect phytoplankton dynamics? *Journal of the North American Benthological Society*, **14**, 616–630.
- Schooler S.S., Salau B., Julien M.H. & Ives A.R. (2011) Alternative stable states explain unpredictable biological control of *Salvinia molesta* in Kakadu. *Nature*, **470**, 86–89.
- Thomaz S.M., Bini L.M. & Bozelli R.L. (2007) Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia*, **579**, 1–13.
- Thomaz S.M., Bini L.M., Pagioro T.A., Murphy K.J., Santos A.M. & Souza D.C. (2004) Aquatic macrophytes: diversity, biomass and decomposition. In: *The Upper Paraná River and its Floodplain: Physical Aspects, Ecology and Conservation* (Eds S.M. Thomaz, A.A. Agostinho & N.S. Hahn), pp. 331–352. Backhuys Publishers, Leiden.
- Thomaz S.M., Carvalho P., Padial A.A. & Kobayashi J.T. (2009) Temporal and spatial patterns of aquatic macrophyte diversity in the Upper Parana River floodplain. *Brazilian Journal of Biology*, **69**, 617–625.
- Van Geest G.J., Coops H., Scheffer M. & Van Nes E.H. (2007) Long transients near the ghost of a stable state in eutrophic shallow lakes with fluctuating water levels. *Ecosystems*, **10**, 36–46.
- Yarrow M., Marin V.H., Finlayson M., Tironi A., Delgado L.E. & Fischer F. (2009) The ecology of *Egeria densa* Planchon (Liliopsida: Alismatales): a wetland ecosystem engineer? *Revista Chilena de Historia Natural*, **82**, 299–313.

(Manuscript accepted 2 May 2012)