Juan José Rosso*, [1], Alejandro Sosnovsky[2], Armando M. Rennella[3]
and Rolando Quirós[3][†]

[1]Centro de Estudios Transdisciplinarios del Agua (CETA), Facultad de Ciencias Veterinarias,
Universidad de Buenos Aires, Av. Chorroarín 280, CP1427 Buenos Aires, Argentina;
e-mail: plurosso@yahoo.com.ar
[2]Grupo de Evaluación y Manejo de Recursos Ícticos, Centro Regional Universitario Bariloche,
Universidad Nacional del Comahue, Quintral 1250, R8400FRF San Carlos de Bariloche, Argentina
[3]Área de Sistemas de Producción Acuática, Departamento de Producción Animal,
Facultad de Agronomía, Universidad de Buenos Aires. Av. San Martín 4453, CP (1417),
Buenos Aires, Argentina

Research Paper

Relationships between Fish Species Abundances and Water Transparency in Hypertrophic Turbid Waters of Temperate Shallow Lakes

key words: South America, Pampa plain, freshwater ecosystems, Secchi disc, fishes

Abstract

We explored the relationships between Secchi disc depth and the abundance of fish species in very shallow, hypertrophic, turbid waters of Pampa Plain lakes, Argentine.

We tested whether the abundance of any of the species present was associated with water transparency for lakes where water transparency, as measured by Secchi disc depth, ranged from 0.1 to 0.4 m. Overall, the abundance of five species (*Cnesterodon decemmaculatus*, *Jenynsia multidentata*, *Corydoras paleatus*, *Pimelodella laticeps* and *Odontesthes bonariensis*) seemed to be affected by this narrow gradient in water transparency. These findings represent an interesting result for turbid hypertrophic environments where narrow ranges in water transparency are traditionally neglected as important factors for fishes. We show, however, how water transparency patterns may be still important for some species in highly turbid waters with extremely narrow gradients in Secchi disc depth.

1. Introduction

Optical properties of lakes are important regulatory parameters of the abundance and distribution of aquatic organisms (Wetzel, 2001). For instance, light has many subtle effects on fish distribution patterns both within and between lakes (Moyle and Cech, 2004). The impacts of turbidity on fish depend largely on the visual adaptations and life-strategy of the concerned species, influencing their capability of performing in environments of varying turbidity (Sandström, 1999). In aquatic consumers that use vision to detect their prey, water transparency constraints affect reaction distance (Miner and Stein, 1996; Vogel and Beauchamp, 1999), encounter rates (Turesson and Brönmark, 2007) and finally consumption rates (Utne-Palm, 2002). Environments where fish abundance and distribution were found to vary as a consequence of water transparency dynamics are as diverse as coastal areas

---

* Corresponding author

(Sandström and Karås, 2002), ancient lakes (Plisnier et al., 2009), large reservoirs (Gido et al., 2002), natural lakes (Lind et al., 1994; Dockendorf and Allen, 2005), estuaries (Blaber, 1997; Maes et al., 1998; Albaret et al., 2004; Akin et al., 2005), floodplain lakes (Rodríguez and Lewis, 1997; Miranda and Lucas, 2004), shallow (>2 m) lakes (Mous et al., 2004; Robillard and Fox, 2006) and rivers (Koné et al., 2003; Barko et al., 2004; Reyjol et al., 2008). The bulk of such information mostly comes from northern temperate and tropical ecosystems. In comparison, information about the effects of water transparency dynamics on fish species in southern temperate ecosystems is more limited (Hart, 1986; Jeppesen et al., 2000).

Although many fish species react to gradients in water transparency, fish also act as ecosystem engineers (Jones et al., 1994) by altering water clarity dynamics through effects on lower trophic levels (including other fishes) (Benndorf et al., 1984; Northcote, 1988; Quirós, 1995) and nutrient dynamics (Tátrai and Istvánovics, 1986; Vanni, 2002; Boros et al., 2009). In particular, a large array of studies have demonstrated that changes in the trophic structure of the fish assemblages, whether via predator or nutrient control, are related to changes in water clarity (e.g., Shapiro and Wright, 1984; Carpenter et al., 1985; Mcqueen et al., 1986; Crowder et al., 1988; Jeppesen, 1998).

In shallow lakes, a basic understanding of under-water optics is essential to understanding the functioning of fish communities (Scheffer, 1998). One of the most outstanding aspects of the Pampa Plain, in the central region of Argentina, is the large number of shallow lakes totalling more than 1,400 water bodies with a maximum length longer than 0.5 km (Canevari et al., 1998). These lakes are very shallow (exceptionally >5 m) and their basins are usually formed by a combination of river and wind action (Tricart, 1973). Instead of alternative stable states (Scheffer et al., 1993), a continuum between three basic states characterizes these lakes, from clear vegetated environments to inorganically-turbid ones and organically turbid where phytoplankton dominates (Quirós et al., 2002a). These three states correspond with differences in phytoplankton assemblage structure and primary production (Allende et al., 2008), trophic structure of the fish assemblages (Quirós et al., 2002b) and land use within the landscape (Quirós et al., 2006). In spite of the broad gradient in water transparency most lakes in the region are extremely turbid (Quirós and Drago, 1999). Among these highly turbid lakes, little is known about how the narrow gradient in water transparency may affect fish species abundances and distributions. There are also comparatively few attempts to study such relationships in very shallow (<2 m), hypertrophic, turbid waters bodies elsewhere in the world (Rowe, 2007).

In this paper we explored the relationship between water transparency and the abundance of fish species in a series of very shallow, hypertrophic, turbid lakes of the Pampa Plain. These lakes are on the most turbid extreme in the continuum highlighted by Quirós et al. (2002a). Hence, our objective was to test whether differences in fish species abundances are associated with water transparency for lakes within the lower range of water transparency.

2. Methods

2.1. Study Site

The study lakes (Mar Chiquita, Gómez, Carpincho and Rocha) are located in the upper reaches of the Salado River (Fig. 1) between 34°21′ and 34°42′ S and 60°39′ and 61°15′ W. This river is an autochthonous lowland system, running through a very flat plain from 78 meters above sea level at its headwater with an overall mean slope of 0.18 m km^{-1} (Bianco, 1998). The study lakes are very shallow (mean depth around 1 m), polymictic, natural water bodies along the main course of the river. Based on mean summer Chl-a concentrations (Table 1) their trophic state indices range between eutrophic to hypertrophic (Håkanson and Boulion, 2001). This river-lake ecosystem usually experiences large

spatial and temporal variation in its main physical and chemical conditions (RENNELLA, 2007; ROSSO, 2008). Hence, we designed our sampling strategy to account for this natural behaviour by ensuring that sampling covered both the spatial and temporal range in variation. Accordingly, we collected monthly (January to March) samples of fish and recorded water transparency during two consecutive summers (2000 and 2001) at five different sites (Mch, GoN, GoE, Crp and Rch) plus in two additional summers (1999 and 2002) at three sites (GoN, GoE and Crp). Sites locations were labelled following the name of the main lake in which they occur (*i.e.* Mar Chiquita (Mch), Gómez north (GoN), Gómez east (GoE), Carpincho (Crp) and Rocha (Rch)).

2.2. Water Transparency

In order to quantify water transparency patterns in these very shallow turbid lakes we measured Secchi disc depth. In temperate lakes, Secchi disc usually fluctuates seasonally (WETZEL, 2001). Therefore, in order to avoid the confounding effects of such seasonal variation in the relationships with fish abundance, we used Secchi disc depth records measured during the peak of the growing season (January to March; South Hemisphere summer). This also allowed us to reduce biases from changes in the seasonal behavior of fishes in relation to the thermal dynamics of waters and photoperiod. Mean Secchi disc depths for each site-summer were estimated ($n = 16$) and then related with the corresponding means of fish species.
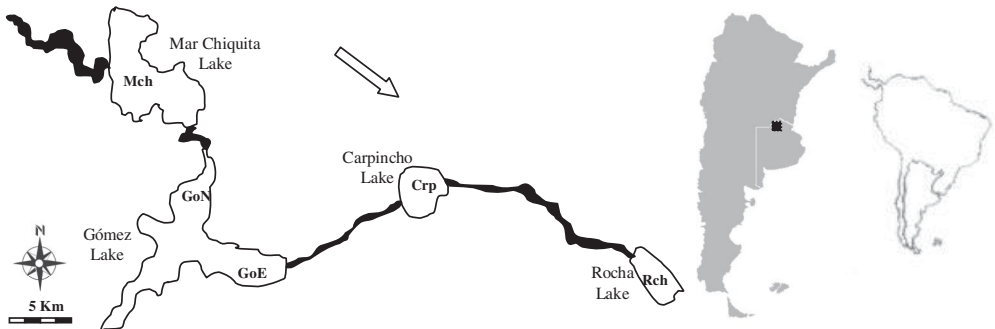

Figure 1.   Schematic diagram of the study area in the upper Salado River, Pampa plain, Argentina. Study sites are labelled as Mch: Mar Chiquita; GoN: Gómez north; GoE: Gómez east; Crp: Carpincho and Rch: Rocha. Open arrow indicates river's main flow direction.

Table 1.   Historical mean summer morphometric and limnological attributes of upper Salado River lakes (Sources: QUIRÓS, 1988; RENNELLA, 2007; ROSSO, 2008).

Lake	Area (km²)	Depth (m)	Secchi (cm)	Chlorophyll-*a* (µg/l)	TP (mg/l)	TN (mg/l)	Conductivity (µS/cm)
Mar Chiquita	50.0	0.9	11	150.98	1.14	5.51	5925
Gómez	40.0	1.2	19	98.88	0.91	5.65	5560
Carpincho	5.0	1.0	21	103.12	0.89	4.92	5341
Rocha	3.6	0.8	18	139.27	1.11	5.50	5200

2.3. Fish Sampling

Large fish species were captured using two multifilament experimental gill nets. Each net consisted of ten panels (15, 21, 25, 30, 35, 40, 52, 60, 75 and 85 mm bar mesh size). All net panels were of equal height (1.4 m) and length (10 m). Gill nets were deployed in the open water zone of lakes during the first hours of evening. Simultaneously, littoral areas were sampled in order to capture small-bodied species. For this purpose we used a bag seine net constructed with 20 m long wings (10 mm mesh) and a 2 m long bag (5 mm mesh). Abundances of fish species were expressed as catch per unit of effort (CPUE). Data from gill net and seine net were not combined. For large fish species, CPUE was estimated as the average number of individuals captured by both gill nets per hour of netting. The abundances of small fish species were quantified by computing the average number of individuals captured by two seine hauls covering 1000 m^2 each. With these data mean abundances of species for each summer at each site were estimated ($n = 16$) and further incorporated in data analyses.

2.4. Data Analysis

Spearman rank correlation coefficients were calculated on log ($x + 1$) transformed variables in order to explore empirical relationships between site-summer means of fish species abundances and Secchi disc depths. In the study lakes, the interactive effects of spatial gradients in water conductivity and $NO_3 : NH_4$ ratio as well as the important interannual hydrological variability affect the abundance and distribution of dominant fish species (*Cyphocharax voga*, *Odontesthes bonariensis*, *Parapimelodus valenciennis* and *Cyprinus carpio*) (ROSSO and QUIRÓS, 2009). Hence, we decided that observed patterns in fish abundance and water transparency should be also tested against these more conspicuous spatial and temporal gradients. Consequently, those species (others than those mentioned above) whose abundances were significantly correlated with Secchi disc depth, were further correlated with water conductivity, water residence time and the $NO_3 : NH_4$ ratio. The latter is considered as an anthropogenic gradient due to the release of organic matter in industrial, urban and municipal effluents to surface waters of this river (ROSSO and QUIRÓS, 2007), and the recognized effects of these effluents on nitrification and denitrification balance (BALLESTER *et al.*, 1999; MARTINELLI *et al.*, 1999; WETZEL, 2001). Data of water conductivity, water residence time and the $NO_3 : NH_4$ ratio were obtained from ROSSO and QUIRÓS (2009). The rationale behind this analysis was to test whether species that were correlated with the extremely narrow gradient in water transparency, showed any evidence of being affected by the wider environmental gradients of the system. This will help, in turn, to evaluate our results within a more complete ecological context. Adjusted *P*-values for the resultant correlation matrix were obtained following the procedure conducted by HOLM (1979). The Holm method constitutes a modest improvement of the familiar and widely used Bonferroni procedure. Adjusted *P*-values were all considered significant if $P < 0.05$.

Besides the correlation analysis, we formulated two basic questions in order to help interpret patterns in fish species abundances and water transparency: 1) Is the mean abundance of each species greater if water transparency is above or below the median? 2) Does the largest abundance of each species occur when Secchi is high or low? This approach is a modification of the one proposed earlier by MYERS and BARROWMAN (1996) to explore stock-recruitment relationships. We found it useful to analyse alternative aspects of the relationships between fish species abundances and water transparency highlighted by the correlation analysis. With this we aim to gain more confidence in our results by looking for consistency between all analyses.

To answer the first question we examined the ratio of the mean abundance of each species when the Secchi disc depth was above the overall median to the mean abundance when Secchi disc depth was below the median. This ratio will equal 1 when the mean abundance of a particular species in all samples taken when secchi disc depth was above the overall median is the same as mean abundance in all samples taken when secchi disc was below the median. This ratio becomes larger when mean abundance is higher in most of the samples from clearer water and *vice versa*. We then performed a Mann-Whitney U test to see if the differences between the mean abundance of each species above and below the median of water transparency data were significant. To examine the second question we computed the rank of Secchi disc depth that gave rise to the largest abundance of each species, *S fishmax*. In order to compare results between species we calculated a relative rank: $r_i = (S\ fishmax_i − 1)/(n − 1)$, where r_i is the relative rank of the *ith* species, *S fishmax*$_i$ is the value of the Secchi disc depth that gave rise to

the largest abundance of the *ith* species and *n* is the number of observations (16). This relative rank lies between 0, implying that the highest abundance of the species occurs at the lowest water transparency (*S fishmax* = 1) and 1, implying that the highest abundance of the species occurs at the highest water transparency (*S fishmax* = 16).

All statistical analyses were performed using the NCCS statistical software (HINTZE, 1998).

3. Results

The study lakes all had extremely low Secchi disc depths (*SD*). Mean site-summer *SD* ranged from 0.10 to 0.40 m with an overall mean *SD* of 0.21 m. Water was generally less transparent in Mar Chiquita and Rocha lakes where mean site-summer *SD* never exceed the overall mean for the system, with values of 0.13 and 0.20 m, respectively (Fig. 2). Conditions clearer than the mean across site-summers were found only in Carpincho and Gómez lakes and maximum values for *SD* occurred in Carpincho and Gómez east (Fig. 2).

A total of 16 species included in 5 orders and 11 families were collected during the surveys (Table 2). Five species (*Cnesterodon decemmaculatus*, *Jenynsia multidentata*, *Corydoras paleatus*, *Pimelodella laticeps* and *Odontesthes bonariensis*) seemed to be aligned with the narrow gradient in *SD* explored in these shallow turbid lakes (Tables 3 and 4; Fig. 3). Four of these species were significantly associated with *SD*. The abundances of small Cyprino-dontiformes *Cnesterodon decemmaculatus* and the inland silverside *Odontesthes bonariensis* were positively related with *SD*. Conversely, the small Siluriformes *Corydoras paleatus* and *Pimelodella laticeps* were more abundant as *SD* decreased. Among the species that were significantly related with *SD*, only *Corydoras paleatus* seemed to be not affected by the major environmental and anthropogenic gradients of the system. Conversely, *Pimelodella laticeps* was highly and significantly correlated with the hydrological, abiotic and anthropogenic
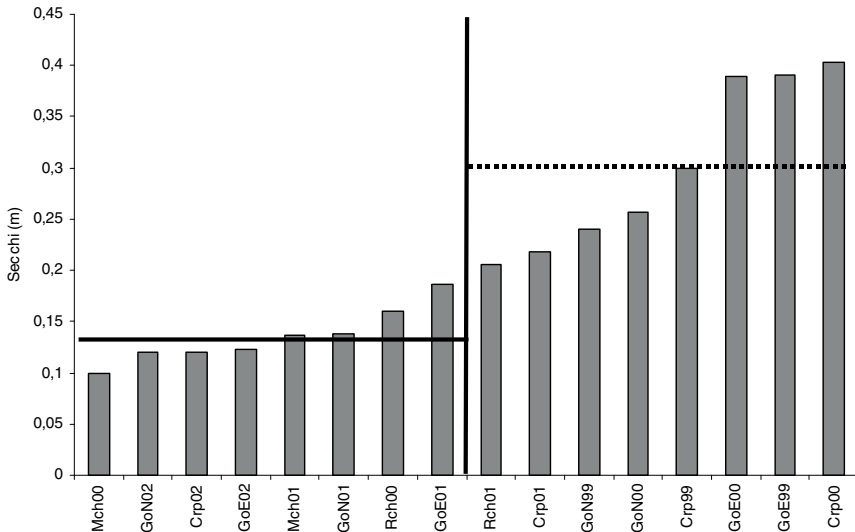

Figure 2.   Mean summer values of Secchi disc depth measured in the upper Salado River lakes during four different summers. Mch: Mar Chiquita Lake, GoE: Gómez Lake, eastern site, GoN: Gómez Lake, northern site, Crp: Carpincho Lake and Rch: Rocha Lake. 99: summer 1999; 00: summer 2000; 01: summer 2001 and 02: summer 2002. Vertical line separates data above and below the median of the series. Horizontal solid and dotted lines represent the means for site-summers *SD* below (0.13 m) and above (0.30 m) the median respectively.

gradients. *Cnesterodon decemmaculatus* was positively related with water residence time of the system (Table 3).

The ratio of mean abundance of each species when the *SD* was above the median to mean abundance when the Sd was below it helped to separate fish assemblages into two main groups. Half of the species collected were more abundant when *SD* was above the median (values larger than 1) whereas the other half were more abundant when *SD* was below the median (values smaller than 1). Nevertheless, our results revealed that the abundance of only three species were significantly higher or lower when *SD* was above the median (Table 4). Abundances of *Odontesthes bonariensis* and *Jenynsia multidentata* were significantly higher when *SD* was above the median. Conversely, the small Siluriformes *Pimelodella laticeps* was significantly more abundant when *SD* was below rather than above the median. Consistent with these results, the largest abundance of several species tended to occur at one extreme of the narrow gradient in *SD* (Fig. 3). Accordingly, *Corydoras paleatus* and *Pimelodella laticeps* had values near 0 in the relative rank of *S fishmax* whereas *Jenynsia multidentata*, *Odontesthes bonariensis* and *Cnesterodon decemmaculatus* displayed values well above 0.5

Table 2. Fish species collected in the upper Salado River lakes. Code: is species code name; Gear: fishing devices used to capture large (gill net) and small (seine net) species.

Order	Family	Taxa	Code	Gear
Siluriformes	Pimelodidae	*Parapimelodus valenciennis*	Pv	gill net
	Heptapteridae	*Pimelodella laticeps*	Pl	seine net
		Rhamdia quelen	Rq	gill net
	Callichthyidae	*Corydoras paleatus*	Cp	seine net
	Loricariidae	*Loricariichthys anus*	La	gill net
Characiformes	Characidae	*Astyanax fasciatus*	Af	seine net
		Astyanax eigenmanniorum	Ae	seine net
		Bryconamericus iheringii	Bi	seine net
		Cheirodon interruptus	Ci	seine net
		Oligosarcus jenynsii	Oj	gill net
	Curimatidae	*Cyphocharax voga*	Cv	gill net
	Erythrinidae	*Hoplias malabaricus*	Hm	gill net
Cypriniformes	Cyprinidae	*Cyprinus carpio*	Cc	gill net
Cyprinodontiformes	Anablepidae	*Jenynsia multidentata*	Jm	seine net
	Poeciliidae	*Cnesterodon decemmaculatus*	Cd	seine net
Atheriniformes	Atherinopsidae	*Odontesthes bonariensis*	Ob	gill net

Table 3. Significant Spearman rank correlation coefficients between fish species abundances and Secchi disc depth. Significant species were further correlated with additional abiotic, anthropogenic and hydrological variables. Adjusted (HOLM, 1979) correlation coefficients = *$P < 0,10$ **$P < 0,05$ and *** $P < 0,01$; a = source: ROSSO and QUIRÓS (2009). Tw: water residence time. Pl: *Pimelodella laticeps*; Cp: *Corydoras paleatus*; Cd: *Cnesterodon decemmaculatus* and Ob: *Odontesthes bonariensis*.

Species	Secchi	Conductivity	NO$_3$: NH$_4$	Tw
Pl	−0.73***	−0.68**	−0.62*	−0.64**
Cp	−0.66***	0.28	−0.08	0.25
Cd	0.63***	0.49	0.04	0.66**
Ob	0.62***	0.53** a	0.71*** a	0.75*** a

Table 4. Mann-Whitney U test results for differences between the mean summer abundances (CPUE) of fish species for samples taken when *SD* was above and below the median of the Secchi disc. The list is intentionally sorted by the ratio between CPUE of species when Secchi disc depth was above the median to CPUE of species when Secchi disc depth was below the median (Above/Below). Dashed line divides the list between species loading a ratio inferior to 1 and those whose exceed this value. NS: not significant. Species codes as in Table 2.

Species	CPUE Above	CPUE Below	Z-Value	*P* value	Above/Below
Cp	2.54	34.51	1.4947	NS	0.07
Pl	2.25	22.58	2.1266	0.033	0.09
Ci	46.37	109.23	1.5429	NS	0.42
Ae	20.28	34.47	1.5228	NS	0.58
Bi	43.38	71.15	1.4178	NS	0.61
La	0.56	0.91	0.5563	NS	0.62
Af	9.49	13.99	1.4178	NS	0.67
Pv	67.95	98.98	0.6826	NS	0.68
Hm	0.61	0.32	1.0361	NS	1.89
Oj	26.28	10.34	0.7877	NS	2.54
Jm	159.41	45.66	−1.7465	0.041	3.49
Ob	107.89	28.79	−1.8379	0.033	3.74
Rq	0.47	0.11	1.5814	NS	4.67
Cc	16.53	3.28	0.3153	NS	5.03
Cv	103.97	12.25	0.0525	NS	8.48
Cd	11.41	1.29	1.5069	NS	8.83

(Fig. 4). Interestingly, two species that did not show any clear pattern with the first analyses, as the piscivores *Hoplias malabaricus* and *Oligosarcus jenynsii*, had their largest abundance at the highest water transparency (Fig. 4).

4. Discussion

Worldwide, some studies have revealed significant relationships between water transparency and fish abundance and distribution in shallow turbid lakes. Mous *et al*. (2004) found that the vertical distribution of zooplanktivorous fish in a shallow turbid lake in the Netherlands was governed by a gradient in Secchi disc ranging from 0.5 to 1.2 meters. Similarly, Rowe (2007) used a large database of New Zealand shallow lakes covering Secchi disc from 0.1 to 9.4 m to study patterns in water clarity in relation to the presence/absence of introduced exotic fish. Changes in the structure of warmwater piscivores communities over a 24-year period was associated with changes in water clarity in Ontario shallow lakes having mean summer Secchi values from 1.1 to 5.5 meters (Robillard and Fox, 2006). The gradients in water transparency explored by these authors are much wider in comparison with our results. Nevertheless, with a narrow and extremely turbid gradient in Secchi disc (0.1 to 0.4 m), we still found that the abundances of some species decreased whilst others increased in relation to spatial and temporal dynamics in water transparency.

The high turbidity in many rivers of South America has probably led to a proliferation of fishes, such as catfishes, that do not rely primarily on vision for prey capture (Moyle and Cech, 2004). Siluriformes fishes thrive successfully under low light climate conditions where vision is of little use. In fact, the activity of some benthic fish has been shown to
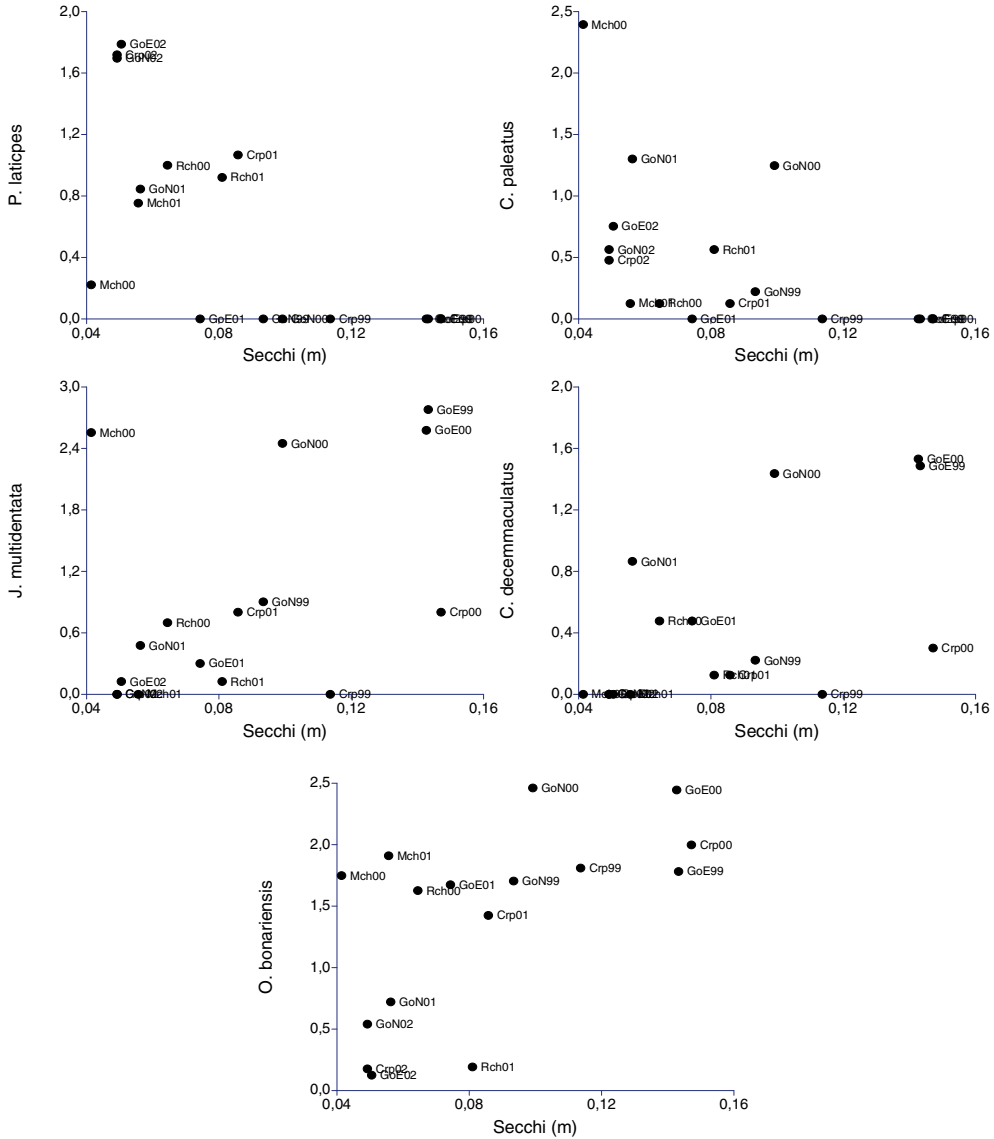
Figure 3. Scatter plots of log transformed fish species CPUE and Secchi depth in the upper Salado River lakes. CPUE of *C. decemmaculatus*, *J. multidentata*, *P. laticeps* and *C. paleatus* estimated from seine net data. CPUE of *O. bonariensis* estimated from gill net data.
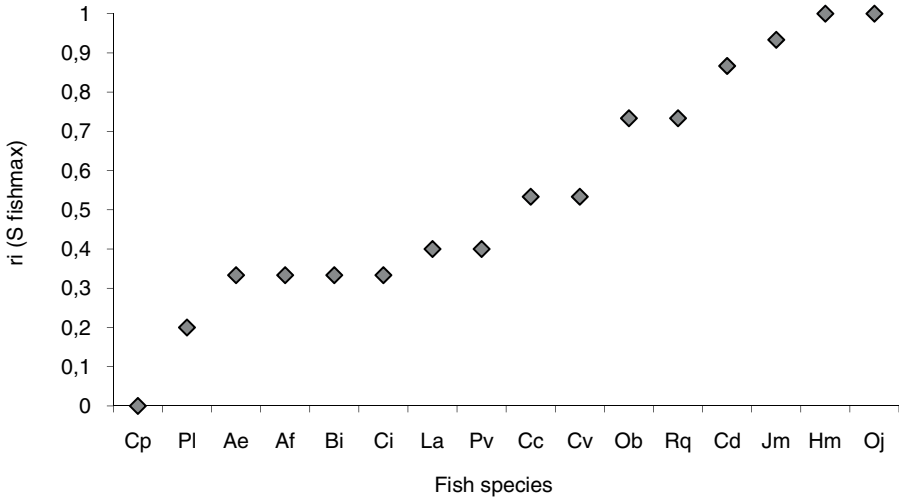
Figure 4.   Relative rank of *S fishmax* ($r_i = (S\ fishmax_i - 1)/(n - 1)$), where r_i is the relative rank of the *ith* species, *S fishmax*$_i$ is the value of the Secchi disc depth that gave rise to the largest abundance of the *ith* species and *n* is the number of observations) for the 16 species collected in the upper Salado River lakes. Species codes as in Table 2.

diminish as light intensity increases being highest when light intensity is near zero (PRENDA *et al.*, 2000). In our study lakes, extremely turbid conditions were associated with higher abundances of Siluriformes benthic species such as *Corydoras paleatus* and *Pimelodella laticeps*. The same positive relationship between abundance of Siluriformes species and water turbidity was found in rivers of Bolivia, Venezuela and Brazil (POUILLY and RODRÍ-GUEZ, 2003).

The low water transparency associated with Siluriformes fishes could also be a consequence rather than a cause. The recycling and resuspension of nutrients from sediments caused by the feeding activity of bottom-dwelling species may help to explain their positive association with phytoplankton biomass (BREUKELAAR *et al.*, 1994) and their negative effects on water transparency (MATTHEWS, 1998). But the role of benthivorous fish in recycling nutrients may be limited in highly productive lakes because here they act as sinks rather than sources (GRIFFITHS, 2006). Nutrient cycling by benthivorous fish may therefore be more significant in less productive lakes (SHAPIRO and WRIGHT, 1984). It has been also shown that the concentration of inorganic suspended solids in the water column increases approximately linearly with the biomass of benthivorous fish (MEIJER *et al.*, 1989). The contribution of *Corydoras paleatus* and *Pimelodella laticeps* to the total fish biomass in the study lakes may be considered negligible (ROSSO, unpublished data). Therefore, the impact of these species on water transparency of these lakes through nutrient and sediment dynamics is likely to be minimal. It is therefore more probable, that these small silurids "select" sites where the lack of water transparency provides them with a competitive advantage over other fish. This could be the result of selective segregation (NILSSON, 1967) from other visually oriented fishes, including predators that inhabit these shallow turbid waters. Such selective segregation could have evolved at some time in the past in response to competition, but whatever its origin, it would minimize contemporary competition as a significant interaction (WOOTTON, 1998).

Despite the generally poor quality of underwater images, fish depend a great deal on sight as a source of sensory information (GUTHRIE and MUNTZ, 1993). Turbidity due to either

inorganic or organic solids will to some extent negatively affect piscivorous Characiformes since their visual activity has been shown to be a crucial element in their ecology (POUILLY *et al.*, 2004). In this study, no significant relationships were found between the abundance of the Characiformes piscivores (*Hoplias malabaricus* and *Oligosarcus jenynsii*) and water transparency. Nevertheless, the low visibility associated with water turbidity could help to explain why these species exhibited their largest abundance at the highest values of water transparency (Fig. 4). In the Pampa Plain, the relative abundance of *Hoplias malabaricus* is higher in clear, shallow lakes where phytoplankton biomass tends to be lowest (QUIRÓS *et al.*, 2002a). Similarly, piscivore species that rely on their visual senses for hunting, dominated the fish assemblages in tropical floodplain lakes with high water transparency (RODRÍGUEZ and LEWIS, 1997). Paradoxically, the same turbidity that may hamper Characiformes piscivores, may favor small Characiformes that are preyed by other fish (PIANA *et al.*, 2006). Accordingly, all the small Characiformes species that we collected in this study (*Astyanax fasciatus*, *Astyanax eigenmanniorum*, *Cheirodon interruptus* and *Bryconamericus iheringii*) were more abundant when water transparency was below the median (Table 4).

Sites where water transparency was higher were characterized by more abundant populations of the Cyprinodontiformes *Cnesterodon decemmaculatus* and *Jenynsia multidentata*. *J. multidentata* is reported to prey on macroinvertebrate organisms attached to or living at the plant surfaces (ESCALANTE, 1983), so visual performance in picking-up potential prey would be important. Similarly, under-water light should be crucial for *Cnesterodon decemmaculatus* which largely prey on attached benthic and periphytic algae (ROSSO, 2006) because turbidity-associated alteration of light is clearly a factor regulating development of periphyton (WETZEL, 2001). In wind-exposed lakes, wind-induced resuspension may largely determine the under-water light climate through attenuation by the water column and periphytic layer (VAN DIJK and VAN DONK, 1991). On the other hand, eutrophication is characterized by a switch from benthic to pelagic dominance of primary productivity (VADEBONCOEUR *et al.*, 2003). Hence, both causes of decrease in water transparency (eutrophication and resuspension) may help clarify the underlying mechanisms behind the positive relationship between Cyprinodontiformes fishes and water transparency in these very shallow hypertrophic turbid lakes.

Surprisingly, the visual zooplanktivore *Odontesthes bonariensis* was positively related with the narrow gradient in water transparency explored in this study. This was a somewhat unexpected result. The trophic cascade theory predicts that the feeding activity of such a size-selective zooplanktivorous species would be conducive to a situation of less herbivory by large zooplankton and high turbidity for phytoplankton biomass (SHAPIRO and WRIGHT, 1984; CARPENTER *et al.*, 1985). Indeed, the negative effect of *Odontesthes bonariensis* on large zooplankton biomass both experimentally (BOVERI and QUIRÓS, 2002) and empirically (QUIRÓS, 1998; RENNELLA and QUIRÓS, 2002) as well as its effects on phytoplankton biomass in biomanipulated lakes (SOSNOVSKY and QUIRÓS, 2009) have already been demonstrated for Pampean lakes. However, *Odontesthes bonariensis* is known to be negatively affected by organic eutrophication from anthropogenic (urban, industrial and municipal) sources (ROSSO and QUIRÓS, 2009). In addition, in hypertrophic highly human-impacted waters where total phosphorous concentration (TP) is highly correlated with the Chl-*a* (QUIRÓS *et al.*, 2002b) this inland atherinid was negatively related with TP (ROSSO and QUIRÓS, 2007). As a consequence, the abundance of the zooplanktivore *Odontesthes bonariensis* would be expected to decline at the highest levels of phytoplankton biomass. This "water quality" effect may help to explain why this visual zooplanktivore was more abundant toward the "clearer" extreme of the narrow gradient in water transparency explored in this study. Hence, the negative impacts derived from eutrophication on the relationships between *Odontesthes bonariensis* and lower trophic levels dynamics should not be disregarded. Similarly, it would be expected that the relative contribution of other zooplanktivore fishes to zooplankton dynamics could be of minor importance at high levels of algal turbidity if zooplanktivore species are prone to be negatively affected by eutrophication.

www.revhydro.com

5. Conclusions

Traditionally, gradients from extremely turbid to clear waters (Quirós *et al.*, 2002a) and alternative stable states (Scheffer, 1998) have been used to explore patterns in the structure of biotic communities of shallow lakes, including fish. We present here empirical evidence to postulate that the abundances of some fish species in highly turbid lakes are also associated with water transparency. This represents an interesting result for turbid hypertrophic environments where narrow ranges in water transparency were traditionally neglected as a controlling force for fish assemblages.

However, our results also showed that the abundances of these species, apart from *Corydoras paleatus*, were not related solely to water transparency but also to major hydrological, abiotic and anthropogenic gradients of the system. Therefore, it is likely that these gradients in combination with water transparency, are more important in structuring the fish assemblage than any of these variables on their own. It is also probably true, that the total contribution of water transparency, albeit significant, will be of relative smaller magnitude when compared with the striking hydrological, abiotic and anthropogenic gradients. Indeed, commonly abundant species such as *Cyphocharax voga*, *Cyprinus carpio* and *Parapimelodus valenciennis* that are significantly affected by these conspicuous gradients (Rosso and Quirós, 2009) were not related at all with water transparency. Nevertheless, this study shows how water transparency patterns may still be important for some species in highly turbid waters with extremely narrow gradients in Secchi disc depth.

6. Acknowledgements

7. References

Akin, S., E. Buhan, K. O. Winemiller and H. Yilmaz, 2005: Fish assemblage structure of Koycegiz Lagoon-Estuary, Turkey: Spatial and temporal distribution patterns in relation to environmental variation.- Estuarine, Coastal and Shelf Science **64**: 671–684.

Albaret, J-J., M. Simier, F. S. Darboe, J.-M. Ecoutin, J. Raffray and L. T. de Morais, 2004: Fish diversity and distribution in the Gambia Estuary, West Africa, in relation to environmental variables. – Aquat. Living Resour. **17**: 35–46.

Allende, L., G. Tell, H. Zagarese, A. Torremorell, G. Pérez, J. Bustingorry, R. Escaray and I. Izaguirre, 2009: Phytoplankton and primary production in clear-vegetated, inorganic-turbid, and algal-turbid shallow lakes from the pampa plain (Argentina). – Hydrobiologia **624**: 45–60.

Ballester, M. V., L. A. Martinelli, A. B. Krusche, R. L. Victoria and P. B. Camargo, 1999: Effects of increasing organic matter loading on the dissolved O_2, free dissolved CO_2 and respiration rates in the Piracicaba River basin, Southeast Brazil. – Water Research **33**: 2119–2129.

Barko, V. A., D. P. Herzog, R. A. Hrabik and J. S. Scheibe, 2004: Relationship among fish assemblages and Main-Channel-Border physical habitats in the unimpounded upper Mississippi River. – Trans. Am.Fish. Soc. **133**: 371–384.

Benndorf, J., H. Kneschke, K. Kossatz and E. Penz, 1984: Manipulation of the pelagic food web by stocking with predacious fishes. – Internat. Revue ges. Hydrobiol. **69**: 407–428.

Bianco, M. R., 1998: El río Quinto Salado del sur. Aportes para su mejor conocimiento. – Editorial Bianco, Junín, Buenos Aires, 196p. ISBN 950-43-9806-5

BLABER, S. J. M., 1997: Fish and Fisheries of Tropical Estuaries. – Chapman and Hall, London. 367 pp.

BOROS, G. Y., I. TÁTRAI, Á. I. GYÖRGY, Á. VÁRI and A. S. NAGY, 2009: Changes in internal phosphorus loading and fish population as possible causes of water quality decline in a shallow, biomanipulated Lake. – Internat. Rev. Hydrobiol. **94**: 326–337.

BOVERI, M.B. and R. QUIRÓS, 2002: Trophic interactions in Pampean shallow lakes: evaluation of silverside predatory effects in mesocosm experiments. – Verh. Int. Ver. Theoret. Angew. Limnol. **28**: 1274–1278.

BREUKELAAR, A.W., E. H. LAMMENS, J. G. BRETELER and I. TÁTRAI, 1994: Effects of benthivorous bream (*Abramis brama*) and carp (*Cyprinus carpio*) on sediment resuspension and concentration of nutrients and chlorophyll-*a*. – Freshw. Biol. **32**: 113–121.

CANEVARI, P., D. E. BLANCO, E. BUCHER, G. CASTRO and I. DAVIDSON, 1998: Los humedales de la Argentina: Clasificación, situación actual, conservación y legislación. – Wetlands International. Publ. 46, Buenos Aires, 208 p.

CARPENTER, S., J. KITCHELL and J. HODGSON, 1985: Cascading trophic interactions and lake productivity. – Bioscience **35**: 634–639.

CROWDER, L. B., R. W. RAPPORTEUR, C. W. DRENNER, C. KER FOOT, D. J. MCQUEEN, E. L. MILLS, U. SOMMER, C. N. SPENCER and M. J. VANNI, 1988: Food web interactions in lakes. – *In*: S. R. CARPENTER (editor), Complex Interactions in Lake Communities. – Springer-Verlag, New York, 119–138.

DOCKENDORF, K. J. and M. S. ALLEN, 2005: Age-0 black crappie abundance and size in relation to zooplankton density, stock abundance, and water clarity in three florida lakes. – Trans. Am. Fish. Soc. **34**: 172–183.

ESCALANTE, A. H., 1983: Contribución al conocimiento de las relaciones tróficas de peces de agua dulce del área platense. III. Otras Especies. – Limnobios **2**: 453–463.

GIDO, K. B., C. W. HARGRAVE, W. J. MATTHEWS, G. D. SCHNELL, D. W. POGUE, and G. W. SEWELL, 2002: Structure of littoral-zone fish communities in relation to habitat, physical, and chemical gradients in a Southern reservoir. – Environment. Biol. Fish. **63**: 253–263.

GRIFFITHS, D., 2006: The direct contribution of fish to lake phosphorus cycles. – Ecol. Freshwat. Fish. **15**: 86–95.

GUTHRIE, D. M. and W. R. A. MUNTZ, 1993: Role of vision in fish behavior. – *In*: T. J. PITCHER (Ed.). Behaviour of Teleost Fishes. – 2nd Edition. Chapman and Hall, Fish and Fisheries Series Nº 7, London.

HÅKANSON, L. and V. V. BOULION, 2001: Regularities in primary production, Secchi depth and fish yield and a new system to define trophic and humic state indices for lake ecosystems. – Internat. Rev. Hydrobiol. **86**: 23–62.

HART, R. C., 1986: Zooplankton abundance, community structure and dynamics in relation to inorganic turbidity, and their implications for a potential fishery in subtropical Lake le Roux, South Africa. – Freshw. Biol. **16**: 351–371.

HINTZE, J., 1998: Number Cruncher Statistical System (NCSS), Version 2000. Users Guide. – Kaysville, Utah, 2311 pp.

HOLM, S., 1979: A simple sequentially rejective multiple test procedure. – Scand. J-Statistics **6**: 65–70.

JEPPESEN, E., 1998: The ecology of shallow lakes – Trophic interactions in the pelagial. – Ph.D. Thesis, National Environmental Research Institute, Silkeborg, Denmark, 420 pp.

JEPPESEN, E., T. L. LAURIDSEN, S. F. MITCHELL, K. CHRISTOFFERSEN and C. W. BURNS, 2000: Trophic structure in the pelagial of 25 shallow New Zealand lakes: changes along nutrient and fish gradients. – J. Plankton Res. **22**: 951–68.

JONES, C. G., J. H. LAWTIN and M. SHACHAK, 1994: Organisms as ecosystem engineers. – Oikos **69**: 373–386.

KONÉ, T., G. G. TEUGELS, V. N. DOUBA, E. P. KOUAMÉLAN and G. GOORÉ BI, 2003: Fish assemblages in relation to environmental gradients along a small west African coastal basin, the San Pedro River, Ivory Coast. – African Journal of Aquatic Science **28**: 163–168.

LIND, O. T., L. O. DÁVALOS-LIND, T. H. CHRZANOWSKI and J. G. LIMÓN, 1994: Inorganic turbidity and the failure of fishery models. – Internat. Rev. ges. Hydrobiol. **79**: 7–16.

MAES, J., A. TAILLIEU, P. A. VAN DAMME, K. COTTENIE and F. OLLEVIER, 1998: Seasonal patterns in the fish and crustacean community of a turbid temperate estuary (Zeeschelde Estuary, Belgium). – Estuarine, Coastal and Shelf Science **47**: 143–151.

Martinelli, L. A., A. B. Krusche, R. L. Victoria, P. B. Camargo, M. C. Bernardes, E. S. Ferraz, J. M. D. Moraes and M. V. Ballester, 1999: Effects of sewage on the chemical composition of Piracicaba River, Brazil. – Water, Air and Soil Pollution **110**: 667–669.

Matthews, W. J., 1998: Patterns in freshwater fish ecology. – Chapman and Hall, London.

McQueen, D. J., J. R. Post and E. Mills, 1986: Trophic relationships in freshwater pelagic ecosystems. – Can. J. Fish. Aquat. Sci. **43**: 1571–1581.

Meijer, M.-L., A. J. P. Raat and R. W. Doef, 1989: Restoration by biomanipulation of Lake Bleiswijkse Zoom the Netherlands first results. – Hydrobiol. Bull. **23**: 49–58.

Miner, J. G. and R. A. Stein, 1996: Detection of predators and habitat choice by small bluegills: effects of turbidity and alternative prey. – Trans. Am. Fish. Soc. **125**: 97–103.

Miranda, L. E. and G. M. Lucas, 2004: Determinism in fish assemblages of floodplain lakes of the vastly disturbed Mississippi alluvial valley. – Trans. Am. Fish. Soc. **133**: 358–370.

Mous, P. J., W. L. T. Van Densen and M. A. M. Machiels, 2004: Vertical distribution patterns of zooplanktivorous fish in a shallow, eutrophic lake, mediated by water transparency. – Ecol. Freshw. Fish **13**: 61–69.

Moyle, P. B. and J. J. Cech, 2004: Fishes: An Introduction to Ichthyology, 5th Edition. – Prentice Hall, Upper Saddle River, 726 pp.

Myers, R. A. and N. J. Barrowman, 1996: Is fish recruitment related to spawner abundance? – Fish. Bull. **94**: 707–724.

Nilsson, N.-A., 1967: Interactive segregation between fish species. – *In*: S. D. Gerking (Ed.). The biological basis of freshwater fish production. – Blackwell, Oxford, 295–313.

Northcote, T. G., 1988: Fish in the structure and function of freshwater ecosystems: a top-down view. – Can. J. Fish. Aquat. Sci. **45**: 361–379.

Piana, P. A., L. C. Gomes and E. M. Cortez, 2006: Factors influencing *Serrapinnus notomelas* (Characiformes: Characidae) populations in upper Paraná river floodplain lagoons. – Neotropical Ichthyology **4**: 81–86.

Plisnier, P.-D., H. Mgana, I. Kimirei, A. Chande, L. Macaza, J. Chimanga, F. Zulú, C. Cocquyt, S. Horion, N. Bergamino, J. Naithani, E. Deleersnijder, L. André, J.-P. Descy and Y. Corne, 2009: Limnological variability and pelagic fish abundance (*Stolothrissa tanganicae* and *Lates stappersii*) in Lake Tanganyika. – Hydrobiologia **625**: 117–134.

Pouilly, M. and M. A. Rodríguez, 2003: Determinism of fish assemblage structure in Neotropical floodplain lakes: influence of whole-lake and supra-lake conditions. – International large river symposium II, conference proceeding, Phnom Phen, Cambodia.

Pouilly, M., S. G. Beck, M. Moraes and C. Ibañez, 2004: Diversidad biológica en la llanura de inundación del río Mamoré. Importancia ecológica de la dinámica fluvial. – Centro de Ecología Simón I. Patiño, Santa Cruz, Bolivia. 383 p.

Prenda, J., S. Rossomanno and P. D. Armitage, 2000: Changes in depth distribution and activity in small benthic riverine fishes under gradually changing light intensities. – Limnética **18**: 75–80.

Quirós, R., 1988: Evaluación del rendimiento pesquero potencial de la República Argentina II: Evaluación por regiones. – Informes Técnicos del Departamento de Aguas Continentales. Instituto Nacional de Investigación y Desarrollo Pesquero. Informe Técnico Nº 8, 9p.

Quirós, R., 1995: The effect of fish assemblage composition on lake water quality. – Lake Reservoir Manage. **11**: 291–298.

Quirós, R., 1998: Fish effects on trophic relationships in the pelagic zone of lakes. – Hydrobiologia **361**: 101–111.

Quirós, R. and E. Drago, 1999: The environmental state of Argentinean lakes: An overview. – Lakes and Reservoirs: Research and Management **4**: 55–64.

Quirós, R., A. M. Rennella, M. Boveri, J. J. Rosso and A. Sosnovsky, 2002a: Factores que afectan la estructura y el funcionamiento de las lagunas pampeanas. – Ecología Austral **12**: 175–185.

Quirós, R., J. J. Rosso, A. Rennella, A. Sosnovsky and M. Boveri, 2002b: Análisis del estado trófico de las Lagunas pampeanas (Argentina). – Interciencia **27**: 1–9.

Quirós, R., M. B. Boveri, C. A. Petracchi, A. M. Rennella, J. J. Rosso and A. Sosnovsky, 2006: The effects of the pampa wetlands agriculturization on shallow lakes eutrophication. – *In*: Tundisi, J. G., Matsumura-Tundisi, T., Sidagis Galli, C. (Eds.), Eutrofização na América do Sul: Causas, conseqüências e tecnologías de gestão. Rede EUTROSUL, PROSUL, São Carlos, Brasil, pp. 1–16.

RENNELLA, A. M. and R. QUIRÓS, 2002: Relations between planktivorous fish and zooplankton in two very shallow lakes of the Pampa Plain. – Verh. Internat. Verein. Limnol. **28**: 887–891.

RENNELLA, A., 2007: Relevancia de las interacciones tróficas en la determinación de la estructura del zooplancton en grandes lagunas pampeanas. – PhD Thesis. FCEyN, UBA.

REYJOL, Y., M. A. RODRÍGUEZ, N. DUBUC, P. MAGNAN and R. FORTIN, 2008: Among- and within-tributary responses of riverine fish assemblages to habitat features. – Can. J. Fish. Aquat. Sci. **65**: 1379–1392.

ROBILLARD, M. M. and M. G. FOX, 2006: Historical changes in abundance and community structure of warmwater piscivore communities associated with changes in water clarity, nutrients, and temperature. – Can. J. Fish. Aquat. Sci. **63**: 798–809.

RODRÍGUEZ, M. A. and W. M. J. LEWIS, 1997: Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. – Ecol. Monogr. **67**: 109–128.

ROSSO, J. J., 2006: Peces pampeanos: guía y ecología. – Literature of Latin America (L. O. L. A.), Buenos Aires, 224 pp.

ROSSO, J. J. and R. QUIRÓS, 2007: Exploring relationships among hydrology, human disturbance and fish abundance in a series of very shallow lowland river lakes. – Proceedings of Multi-level and Multiscale Sustainability Congress, Cochabamba, Bolivia, 1264–1272.

ROSSO, J. J., 2008: Relación entre la abundancia y estructura de la comunidad de peces y el régimen hidrológico en lagunas de la alta cuenca del río Salado. – PhD Thesis. Escuela para Graduados "Alberto Soriano". Facultad de Agronomía, Universidad de Buenos Aires. 97 p.

ROSSO, J. J. and R. QUIRÓS, 2009: Interactive effects of abiotic, hydrological and anthropogenic factors on fish abundance and distribution in natural run-of-the-river shallow lakes. – River Res. Applic. **25**: 713–733.

ROWE, D. K., 2007: Exotic fish introductions and the decline of water clarity in small North Island, New Zealand lakes: a multi-species problem. – Hydrobiologia **583**: 345–358.

SANDSTRÖM, A., 1999: Visual ecology of fish – a review with special reference to percids. – Fiskeriverket Rapport 1999 **2**: 45–80.

SANDSTRÖM, A. and P. KARÅS, 2002: Effects of eutrophication on young-of-the-year freshwater fish communities in coastal areas of the baltic. – Environmental Biology of Fishes **63**: 89–101.

SCHEFFER, M., S. H. HOSPER, M.-L. MEIJER, B. MOSS and E. JEPPESEN, 1993: Alternative equilibria in shallow lakes. – Trends Ecol. Evol. **8**: 275–279.

SCHEFFER, M., 1998: Ecology of Shallow Lakes. – Chapman and Hall, London.

SHAPIRO, J. and D. I. WRIGHT., 1984: Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. – Freshw. Biol. **14**: 371–383.

SOSNOVSKY, A. and R. QUIRÓS, 2009: Effects of fish manipulation on the plankton community in small hypertrophic lakes from the Pampa Plain (Argentina). – Limnologica **39**: 218–229.

TÁTRAI, I. and V. ISTVÁNOVICS, 1986: The role of fish in the regulation of nutrient cycling in Lake Balaton. – Freshw. Biol. **16**: 417–424.

TRICART, J. F., 1973: Geomorfología de la Pampa Deprimida. – Instituto Nacional de Tecnología Agropecuaria, Buenos Aires, Argentina. 202p.

TURESSON, H. and C. BRÖNMARK, 2007: Predator–prey encounter rates in freshwater piscivores: effects of prey density and water transparency. – Oecologia DOI 10.1007/s00442-007-0728-9

UTNE-PALM, A. C., 2002: Visual feeding of fish in a turbid environment: physical and behavioural aspects. – Mar. Freshwater Behav. Physiol. **35**: 111–128.

VADEBONCOEUR, Y., E. JEPPESEN, M. J. VANDER ZANDEN, H. SCHIERUP, K. CHRISTOFFERSEN and D. LODGE, 2003: From Greenland to green lakes: Cultural eutrophication and the loss of benthic pathways in lakes. – Limnol. Oceanogr. **48**: 1408–1418.

VAN DIJK, G. M. and E. VAN DONK, 1991: Perspectives for submerged macrophytes in shallow lake restoration projects in the Netherlands. – Hydrobiol. Bull. **24**: 125–131.

VANNI, M. J., 2002: Nutrient cycling by animals in freshwater ecosystems. – Annu. Rev. Ecol. Syst. **33**: 341–370.

VOGEL, J. L. and D. A. BEAUCHAMP, 1999: Effects of light, prey size, and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. – Can. J. Fish. Aquat. Sci. **56**: 1293–1297.

WETZEL, R. G., 2001: Limnology: Lake and River Ecosystems. Third edition. – Elsevier, Academic Press, 1006 pp.

WOOTTON, R. J., 1998: Ecology of teleost fishes. – Kluwer Academic Publishers, 2nd Edition, 386 pp.