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LONG-TERM HYDROLOGIC VARIABILITY IN A LARGE SUBTROPICAL FLOODPLAIN RIVER: EFFECTS ON COMMERCIAL FISHERIES

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ABSTRACT

We analysed the effects of decadal and annual hydrologic fluctuations on freshwater fisheries catches in the Middle Paraná River for a period of six decades from the 1930s to the 1980s. The climatic fluctuations in this period strongly affected the hydrology of the Middle Paraná River and the characteristics of its flow regime. The magnitude of floods as well as maximum, minimum and mean water levels increased progressively from 1930s until the 1980s concomitantly with increasing frequency and intensity of El Niño Southern Oscillation events that resulted in differentiation of distinct hydrological periods. The flood pulses were significantly more frequent and of greater magnitudes during the 1970s and 1980s. These large floods resulted in increased commercial fish catches in the 1980s, possibly because of enhanced recruitment. Specifically, large floods increased the commercial fish catches 2 years later. This effect was stronger for species that use floodplain habitats as areas of reproduction and larval nurseries, such as *Prochilodus lineatus*. We conclude that the natural flow regime of the Paraná River and perhaps other large subtropical rivers must be preserved in order to sustain their productive fisheries. Copyright © 2016 John Wiley & Sons, Ltd.

KEY WORDS: climatic fluctuations; historic hydrologic fluctuations; flow regime; freshwater fisheries; Middle Paraná River (Argentina)

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INTRODUCTION

The effects of seasonal flow dynamics (alternating high-water and low-water) on aquatic ecosystems are well documented, especially in subtropical and tropical floodplain rivers. These water-level fluctuations govern the degree of lateral connections and facilitate exchange of water, nutrients and organisms between the main river channel and adjacent floodplain as formulated in the 'flood pulse concept' (Junk *et al*., 1989). Furthermore, seasonal flooding is considered to be the key environmental factor that drives the community structure and distribution of aquatic organisms in the floodplain (Junk *et al*., 1989; Neiff, 1990; Górski *et al*., 2011; Górski *et al*., 2013). Connectivity among floodplain habitats increases the number of natural nurseries for fish and drives high species diversity (Winemiller, 2004).

Flood pulse attributes, such as the duration and magnitude of inundation, are thought to be the main factors underlying the importance of floodplains for the spawning and growth of riverine fish that utilize floodplain habitats (Bailly *et al*., 2008; Górski *et al*., 2010; Wu *et al*., 2013; Górski *et al*., 2016). Furthermore, commercial fish stocks are expected to be linked to natural pulse dynamics (Moses, 1987; Górski *et al*., 2012). Several migratory neotropical fish species are characterized by a high degree of synchronization between their reproductive cycle and seasonal river flow dynamics (Agostinho *et al*., 2004; Agostinho *et al*., 2007; Bailly *et al*., 2008); a large proportion of these species are large-bodied and of high commercial value in multiple South American countries, including Argentina.

The fish fauna of the Paraná River has faced increased pressure during recent decades because of development of commercial fishing and possible environmental changes caused by the construction of dams in the Upper Paraná River. No quantitative studies exist to assess these effects on migratory fish in the Middle Paraná River. Furthermore, these direct anthropogenic effects are expected to be superimposed by the projected climatic changes (IPCC, 2014). The climate variability during the past century in South America and its impact on the hydrological regimes of some of its major rivers has been studied (García and Vargas, 1998; Giacosa *et al*., 2000; Barros *et al*., 2006); however, how the reported changes in the hydrology of the Paraná River have affected its biota and specifically the fish fauna remains unknown. Thus, there is an urgent need to understand drivers of populations of commercially important species in order to implement informed management strategies.

A total of 240 native fish species were recorded in the Paraná River in Argentina, whereas commercial fisheries

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are dominated by only 12 large-bodied migratory species (López, 2001). The fish catches are dominated by large Characiforms and Siluriforms, with predominance of *Prochilodus lineatus*, *Leporinus obtusidens* *Salminus brasiliensis*, *Pseudoplatystoma fasciatum* and *P. corruscans*. These species are known for their long-distance migration, which might encompass the whole basin (Bonetto *et al*., 1969; Sverlij and Espinach Ros, 1986). They reproduce during summer in lotic habitats of the main channel and use different floodplain habitats as nurseries for larvae and juveniles (Baigún *et al*., 2003). Thus, the availability of these floodplain habitats is crucial to the ability of these species to complete their life cycles (e.g. Quirós and Cuch, 1989 showed that the total catches of *Prochilodus* increased with the increase of floodplain areas available and/or the frequency of inundations).

The fisheries in the Middle Paraná River contribute the majority of the continental fishing production of Argentina (Baigún *et al*., 2003). Espinach Ros (1993) estimated this production at 15 000 tons per year. Furthermore, fish meat contributes a substantial fraction of protein in the diets of many people in this region (FAO, 2014). In addition, riverine fisheries are an important source of income for the tourism industry in the regions adjacent to the Middle Paraná River as well as fish exports. Between 2007 and 2013, the volume of riverine fish exported generated incomes of approximately $113M (FAO, 2014).

Studies considering the effects of flow regimes on riverine fisheries on large temporal scales (along a decade or more) are uncommon because of the lack of empirical data at such time scales (Górski *et al*., 2012). Most of the available studies assess the effects of flow regulation because of the constructions of dams (e.g. Agostinho *et al*., 2004; Bailly *et al*., 2008; Górski *et al*., 2012). Official fishing statistics may be useful for evaluating fish population dynamics on large temporal scales and predicting future catches; unfortunately, however, they are often of poor quality and quantity (Welcomme, 1985; Gehrke *et al*., 2011).

The collection of data on commercial fish catches in the Paraná River in Argentina began around 1930 and was maintained with sufficient completeness and quality for nearly 50 years. This valuable information was used in the present study to analyse the effects of decadal and annual hydrologic fluctuations in the past century on the fisheries catch in the middle reach of the Paraná River. We first examined flow regime changes between 1930 and 1980, with focus on the variations of flood pulses (e.g. magnitude, frequency, duration and timing). Secondly, we assessed how the commercial fish catches varied in the same time period to discern the effects of flood pulse characteristics on them.

Given that the hydrologic fluctuations are key factors structuring riverine fisheries, because they affect reproduction, survival and recruitment of the main commercial species, we expected that both total biomass and composition of catches change in relation to annual and decadal flow regime variations. Specifically, we expected that more frequent and larger floods, producing an increased connectivity between the main channel and floodplain habitats, result in higher catches in subsequent years because of an enhanced recruitment of commercially important fish species.

METHODS

Study area

The Paraná River is the ninth river in the world in terms of its mean annual discharge at the mouth, (18 000 $m^3 s^{-1}$; Latrubesse, 2008) and its basin is the second largest in South America with an area of 2,00 000 km^2. The alluvial plains in its middle reaches are a vast system characterized by numerous channels, lakes, islands and swamps that are mostly unaltered and unpopulated by humans (Iriondo *et al*., 2007).

Our study area extends along the Paraná River and its floodplain between 27–32° of latitude south and 58–60° of longitude west, from the confluence of the Paraná River with its main tributary the Paraguay River to the city of Diamante (Figure 1). In the upper limit of the study area, the Paraná River is characterized by the discharge of approximately 17 000 $m^3 s^{-1}$, which is a sum of the discharges of the Upper Paraná River (~12 400 $m^3 s^{-1}$) and the Paraguay River (~3800 $m^3 s^{-1}$). The hydrochemistry of main channel and secondary/minor floodplain courses (lotic habitats) in the middle reach is adequate for fish life as well as aquatic biota, according to international standards for water quality (Hammerly 2011). The Middle Paraná River is highly turbid as it carries large volume of suspended sediments with high content of fine material (suspended solids can reach concentrations of 4.500 mg l^{-1}; Drago and Amsler, 1988). This high turbidity is specific for the lower river and distinguishes it from the upper basin (Paoli and Cacik, 2000).

The Paraná River in the middle reaches is characterized by wide and productive *Potamon* and an extensive and complex adjacent floodplain. This reach is unimpounded, different from the Upper Paraná in Brazil, where numerous large dams were built since the end of the 1960s. In the Middle Paraná River, the alluvial floodplain spreads mostly along the western bank of the main river channel and covers an area of approximately 13 000 km^2 (Drago, 1989). The floodplain is formed by numerous secondary channels and accommodates multiple lakes and swamps. The fisheries catches analysed in the present study were obtained along this river corridor where the bulk of freshwater fisheries of Argentina is concentrated (Fuentes and Quirós, 1988). The Middle Paraná River is situated in a moderate/warm-humid Neotropical climatic zone. The mean annual temperatures are approximately 19 °C. The annual precipitation is

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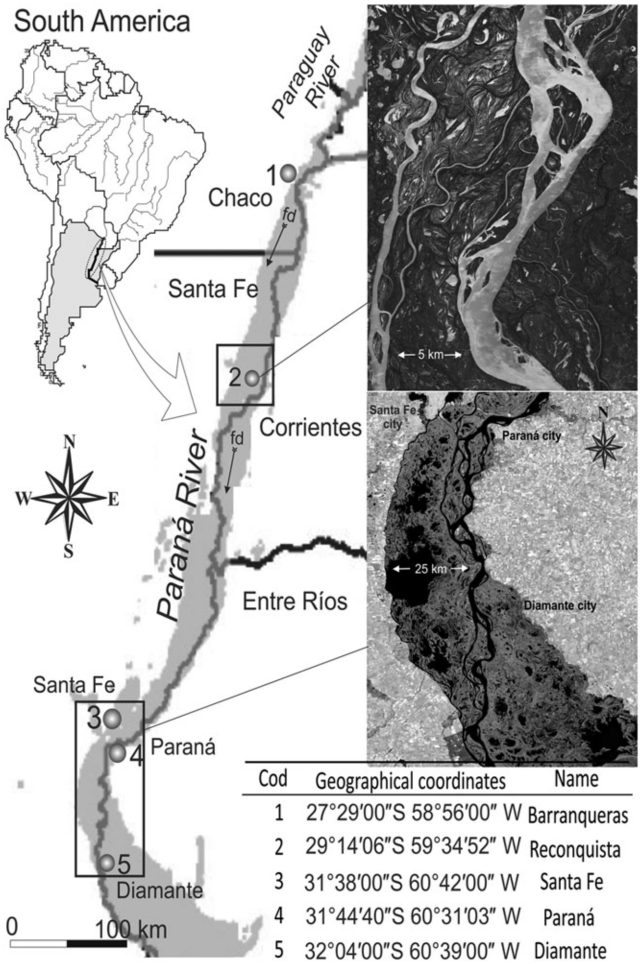

Figure 1. Study area (the Middle Paraná River in Argentina). Numbers indicate ports from which commercial fisheries data were obtained. *fd*; flow direction

approximately 900 mm, with rains predominantly from October until April (73%) (Paoli and Cacik, 2000).

Hydrologic data and their analyses

Daily water levels that were used to characterize the hydrological changes along the study period (1930s to 1980s) were supplied by the Dirección Nacional de Vias Navegables of Argentina and were recorded at the Santa Fe Port gauge (Figure 1). The natural flow regime of the Paraná River is characterized by a high-water-level season associated with intensive rains in the upper basin in the austral summer–autumn (December–April) and a low-water period in the early austral spring (September–October) (Giacosa *et al*., 2000). For the analyses of variables of the hydrological regime within the study area, the height of 4.5 m was selected as the reference level when river water begins to flood the adjacent floodplain (overflow level and flood pulses) and the height of 2.3 m was selected as the reference of disconnection of most of the lakes in the floodplain (Paira, 2003). High-water-level periods that were between bank overflow (4.5 m) and 3.0 m were referred to as flow pulses (Tockner *et al*., 2000).

For analyses of the flow regime of the river within the study period (1935–1983), we identified 18 relevant hydrological variables obtained from the daily data records (Table I). For the analysis of the associated temperatures, daily air temperatures were obtained from Servicio Nacional Meteorológico of Argentina in Santa Fe. To build and compare flow typology among years, we used cluster analysis (Ward's algorithm; Ward, 1963). To eliminate multicollinearity, significant collinear relationships were identified between flow regime variables (Pearson's $r > 0.6$) and the redundant variables were omitted in the final analyses (Table I). Subsequently, we used principal component analysis (PCA) and cluster analysis to assess overall similarity of flows among years (using nine selected variables).

Fisheries data and analyses

The catch data of commercial fisheries in the Middle Paraná River for the study period 1935–1983 were obtained from two sources: Ministerio de Agricultura and Dirección Nacional de Pesca Continental (Argentina). The obtained data consisted of landing reports on monthly/annual catches (total and by species) registered by the Prefectura Naval Argentina in ports along the Paraná River. The catches were registered by species in kilograms (kg) or tons for each port along the fluvial corridor of the Middle Paraná River and later summed up in a monthly catch value by species and port (Fuentes and Quirós, 1988). Unfortunately, information on exact fishing effort was unavailable. Furthermore, values registered on the official statistical catches do not include catches by sports and artisanal fishers (Baigún *et al*., 2003). Because there were no major changes in the applied types of fishing gear, and hence, catchability of species should not change substantially, the data are still useful to explore temporal developments of catches in relation to hydrology. Fish catches were characterized by total and individual species biomass (kilograms and tons). The ports that were used in the analyses were selected based on the representativeness of the Middle Paraná River and completeness of the data they have registered in the period 1935–1983.

The differences in total fish catches among decades were tested using a non parametric one-way permutational analysis of variance (PERMANOVA software v.1.6; Anderson, 2001). Pairwise posteriori comparisons were carried out to assess which decades significantly differed. During the whole study period, a total number of 19 fish species were captured. To assess the variation of contribution of different species to the total catch in selected ports, we calculated the proportion (%) for each species per year for each port. Seven

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Table I. Hydrological and temperature variables selected to characterize the flow regime

Group	Code of variable	Description of variable
Flood size and duration	***Hmax***	Maximum water level (m) measured at Santa Fe Port
	HmeanFlood	Mean water level at Santa Fe Port during flooding
	SupFlood	Duration of the flood for Hmeanflood (flood surface; over the overflowing threshold)
	Duration	Number of days in high waters, flood (>4.5 m)
Average flow period	***HmeanWetDays***	Water levels below 4.5 m
	Hmean	Annual average water level
	WetDays	Number of days between the overflowing threshold (<4.5 m) and disconnection threshold (>2.3 m)
Low-flow period	*Hmin*	Minimum water level measured at Santa Fe Port
	HmeanDryDays	Water levels below 2.3 m (dry period)
	DryDays	Number of days below the disconnection threshold (<2.3 m)
Flood timing	***DateStartFlood***	Date of the start of flooding, Julian days
	DateHmax	Date of maximum water level at Santa Fe Port
	DateEndFlood	Date of the end of flooding
	Delay	Delay of the flood (number of periods of 15 days between October 1 and the beginning of the flood). Following Oliveira *et al*., 2014
Associate temperatures	***TStartFlood***	Water temperature on the first day of flooding
	TendFlood	Water temperature on the last day of flooding
	TmeanFlood	Mean water temperature during flooding
	TmeanAnnual	Annual average temperature

Significant and not collinear selected variables highlighted in bold.

fish species that accounted for approximately 75% of the total of commercial catches in the Middle Paraná River in analysed period were selected. Six of them represent >9% of the total catch and also occur in all decades analysed. In addition, *Leporinus obtusidens* was included because of its very high commercial and biological importance (Table II). Subsequently, calculated percentages were arcsine-transformed (arcsine $\sqrt{[\%/100]}$) per species. The canonical analysis of the principal coordinates (CAP software v1.0; Anderson, 2004) was used to assess temporal patterns of similarity in the structure of fish catches (arcsine-transformed) among decades.

To analyse the effects of flow regime variables on the variation of fish commercial catches in the Middle Paraná River, we used distance-based redundancy analyses (dbRDAs) (PRIMER-E software, McArdle and Anderson, 2001; with the add-on package PERMANOVA+, Anderson *et al*., 2008). In the case of zero catches, these were considered not as true zeroes, but as catch levels below detection level and were set to half the level of the minimum non-zero catch per species (Górski *et al*., 2012). dbRDA is a 'semi-parametric' analysis and does not assume normality or homogeneity of variances, but predictor variables were log10-transformed when necessary to improve the linear fit of the data. These analyses were performed using lag periods of 0–6 years, exploring the possible delay in the response of the fish commercial catches to flow regime characteristics, in relation to recruitment. Subsequently, we assessed correlations between fish catches and specific flood variables that were identified as significant explanatory variables. To avoid multicollinearity, significant collinear relationships were identified between predictor variables (Pearson's $r > 0.6$) and the redundant predictor variables were omitted.

Permutational analysis of variance, canonical analysis of the principal coordinates, cluster analysis and dbRDA differences were tested based on the Steinhaus/Bray–Curtis distance matrix (Legendre and Legendre, 2012). The probability values were obtained for predictor variables by 9999 random permutations (Manly, 1997). Pearson correlations, cluster analysis and PCA were carried out with the R statistical software (R Development Core Team, 2011). Significance was determined at $\alpha < 0.01$ in all analyses.

RESULTS

Flow regime variability

Substantial variations in flow regime among analysed decades were observed (Figure 2A). The average water level at the Santa Fe Port gauge varied between 2.82 m (1940s) and 4.23 m (1980s) (Figure 2A). All decades, except the 1970s and 1980s, were characterized by high-water-level periods starting in December with flood peaks in February, March and April, whereas the lowest water levels were recorded in August and September. The maximum water levels registered in each decade were 5.9 m (1930s), 5.83 m (1940s), 6.12 m (1950s), 6.94 m (1960s), 6.36 m (1970s) and 7.35 m (1980s). The floods were larger and more frequent during 1970s and 1980s, with one extraordinary event in 1983, when water levels peaked up to 7.35 m. The 1980s was an exceptionally wet decade with significantly higher rates of flooding, different from all other decades analysed and characterized by flooding every year (1304 flooded days in total: Figure 2A). There was also

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Table II. Species of freshwater fish catches registered in the official statistics

Species	Code	Common name	Family	Abundance in the catch (%)
***Pseudoplatystoma* sp.**	***Pse sp***	**Surubí**	**Pimelodidae**	**14.32**
Luciopimelodus pati	***L pat***	**Patí**	**Pimelodidae**	**13.83**
***Colossoma* sp.**	***Col sp***	**Pacú**	**Characidae**	**12.44**
Pimelodus albicans	***P alb***	**Bagre blanco**	**Pimelodidae**	**10.07**
Prochilodus lineatus	***P lin***	**Sábalo**	**Prochilodontidae**	**9.65**
Salminus brasiliensis	***S bra***	**Dorado**	**Characidae**	**9.47**
Zungaro sp.	*Zun sp*	Manguruyú	Pimelodidae	5.28
Pterodoras granulosus	*P gra*	Armado común	Doradidae	5.22
Pimelodella sp.	*Pim sp*	Bagarito	Pimelodidae	4.37
Pimelodus maculatus	*P mac*	Bagre amarillo	Pimelodidae	4.31
Leporinus obtusidens	***L obt***	**Boga**	**Anostomidae**	**3.76**
Ageneiosus sp.	*Age sp*	Manduví	Auchenipteridae	3.16
Odontesthes bonariensis	*O bon*	Pejerrey	Atherinopsidae	1.58
Potamotrygon sp.	*Pot sp*	Raya	Potamotrygonidae	1.40
Brycon sp.	*Bry sp*	Pirapitá	Characidae	0.61
Astyanax sp.	*Ast sp*	Mojarra	Characidae	0.24
Lycengraulis grossidens	*L gro*	Anchoíta	Engraulidae	0.12
Serrasalmus sp.	*Ser sp*	Palometa	Characidae	0.12
Hoplias malabaricus	*H mal*	Tararira	Erythrinidae	0.06

Codes used in graphs, common name, family and % of the total catches; species selected for analyses are indicated in bold.

substantial variation in flow patterns among specific years (Figure 2B).

Cluster analysis of the flow regime of the Middle Paraná River in the study period (1935–1983) resulted in three clearly distinguishable groups (Figure 3). Among 43 years analysed, 31 were characterized by floods (of different magnitude). Group 1 consists of the largest floods with maximum water levels between 5 and 7.35 m and of long durations (40 to 365 days; floods mainly in summer). The entire decade of 1980s belongs to this cluster. Group 2 is composed of flood pulses of low magnitude and a very brief duration (between 7 and 49 days). Group 3 includes years that were characterized by only flow pulses with maximum heights between 3.72 and 4.27 m.

The PCA using the most significant and non-collinear flow variables (Table I) resulted in 46% of the total variance explained by axis 1 and 23% explained by axis 2. Axis 1 was strongly correlated with Hmax, HmeanWetDays, DateStartFlood, TstartFlood, TmeanFlood and SupFlood, that is, variables that describe the size and duration of the floods and associated temperatures. Axis 2 was correlated with DryDays, WetDays and TmeanAnnual, variables that describe the low-flow period (Figure 4A).

The PCA closely reflected groups obtained in the cluster analysis (Figure 4B). Group 1 included years with the biggest flood pulses, with maximum water levels between 5.2 and 7.3 m and of long durations. Group 2 was characterized by years with flood pulses of short duration, with maximum

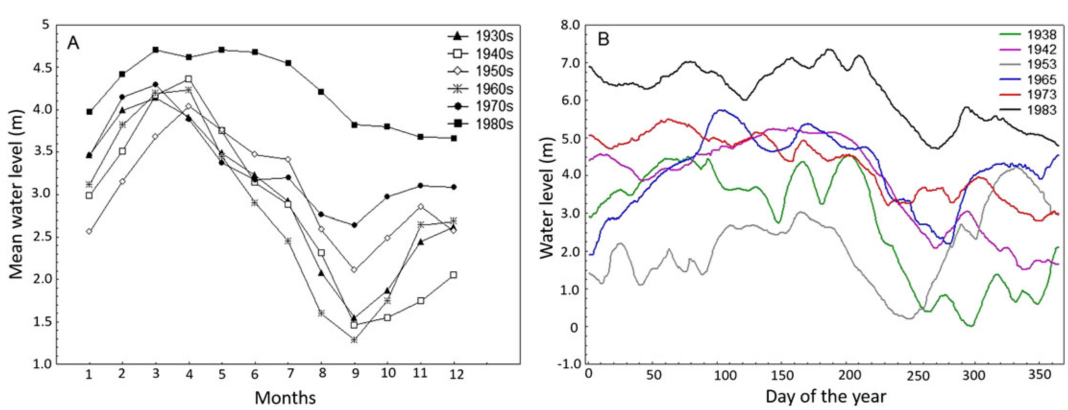

Figure 2. (A) Monthly average water level at the Santa Fe Port gauge for analysed decades. (B) Daily water level for some selected years: 1938, 1942, 1953, 1965, 1973 and 1983. [Colour figure can be viewed at wileyonlinelibrary.com]

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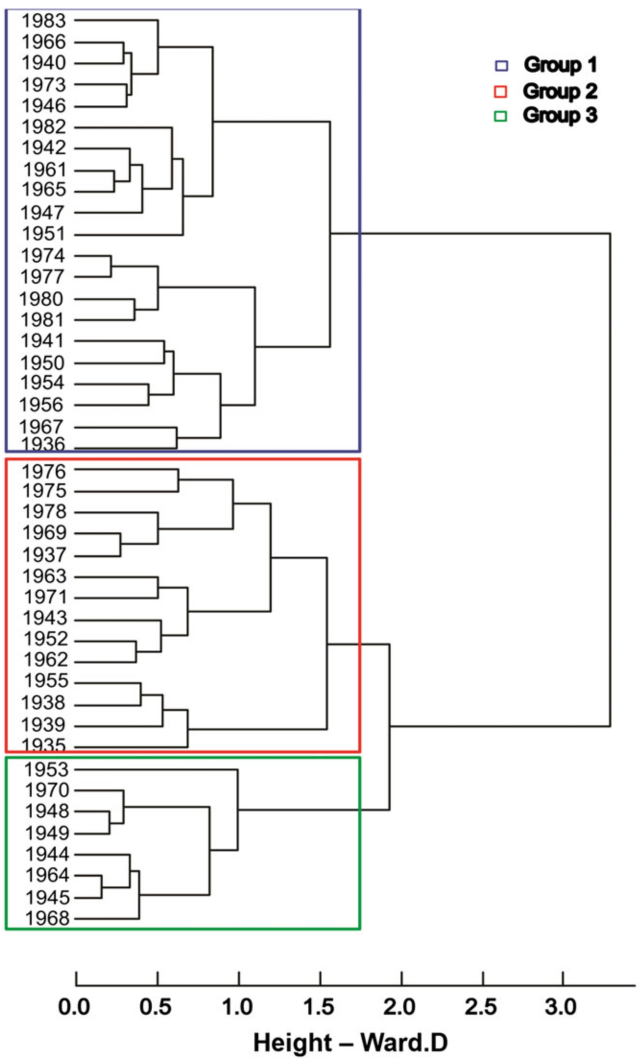

Figure 3. Cluster analysis (Ward method; Ward, 1963) of flow regime in the study period (1935–1983) using 18 selected hydrological variables (Table I). [Colour figure can be viewed at wileyonlinelibrary.com]

water levels between 4 and 5.9 m, but with flood pulses and predominance of wet days. Group 3 represented only flow pulses, with maximum levels between 3.7 and 4.3 m and with predominance of dry days.

Fish catches: interdecadal changes

The largest catches of the commercial fish in the Middle Paraná River were obtained in the 1980s (~1300 tons) followed by the 1940s (~800 tons, Figure. 5). The 1930s is the decade that was characterized by the lowest catches (~300 tons, Figure 5). The difference in the total catches between decades was statistically significant (PERMANOVA; $F = 2.965$, $p < 0.01$). In the 1980s, the catches were significantly higher compared with the other decades (Figure 5), followed by the 1940s, 1950s, 1960s and 1930s. The observed significant increase in commercial catches was associated with the increase of the minimum, maximum and mean water levels in the river (Santa Fe Port gauge; Figure 5).

Canonical analysis of principal coordinates indicated significant temporal differences in the species compositions of catches in the analysed decades (tr(Q_m′HQ_m) = 1.469, $p < 0.001$; Figure 6). Species composition of the catches gradually changed with the decades (Figure 6A). The 1960s, 1970s and 1980s clustered more closely, whereas 1930s differed significantly from other decades in terms of species composition of the catches. *S. brasiliensis* was abundant in the catches from the first two decades. The highest catches of *Colossoma* sp. were recorded in the 1940s, diminishing significantly in the 1960s. *L. obtusidens* and *P. lineatus* showed a progressive increase in the catches from 1960s onwards and reached the highest catches in the last two decades.

Fish catches: interannual changes

Distance-based redundancy analyses models that best explained the structure of commercial fish catches indicated that fish catches in a particular year were related to flood characteristics occurring 2 years before (lag 2; Figure 7). This model significantly explained 43% of the variance in fish catches (Figures 7 and 8).

Within the lag 2, axis 1 explained 30.6 % of the total variance and was strongly positively correlated with the flood height (HmeanFlood) and negatively with minimum water level (Hmin) (Figure 8). Variables associated with temperature such as TmeanAnnual and TStartFlood correlated with axis 2 (which explained 11.01 % of the variance; Figure 8). *S. brasiliensis* was correlated with the HmeanFlood, while *L. obtusidens* was associated with Hmin. Furthermore, *P. lineatus*, *Pseudoplatystoma* sp., *Luciopimelodus pati* and *Pimelodus albicans* were associated with mean annual temperature.

DISCUSSION

Flow regime variability

The flow regime of the Middle Paraná River varied substantially through the 20th century. Distinct hydrological periods were identified in analysed period with progressive increases of the mean, maximum and minimum water levels from the 1930s until the 1980s. The flood pulses were significantly more frequent and of major levels in the 1970s and 1980s. South-eastern South America is the region that presents the highest increase in the annual precipitation during the 20th century (Giorgi, 2003). In the south of Brazil

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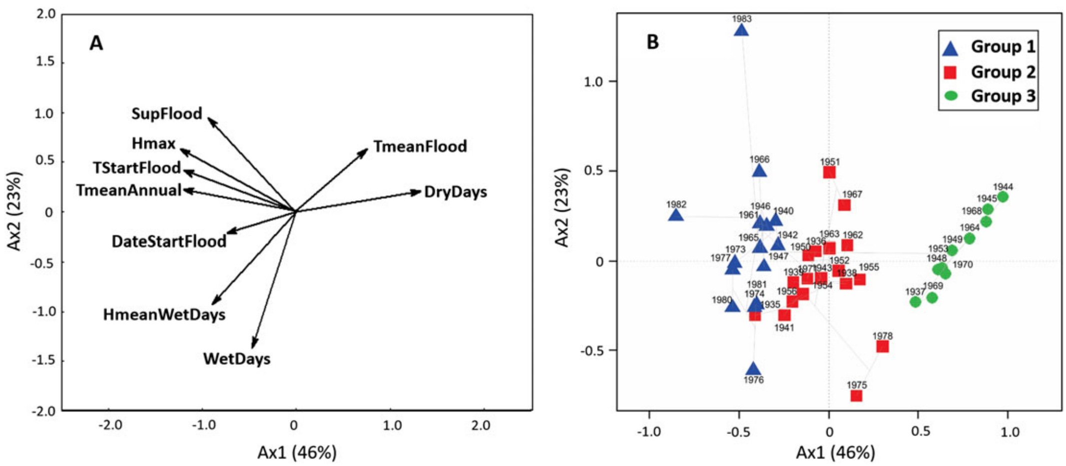

Figure 4. (A) Flow and temperature variables correlating most with Ax1 and Ax2 of the principal component analysis (PCA) of the years 1935–1983. (B) Cluster analysis of individual years; flow regime groups correspond to PCA analysis in Figure 4A. [Colour figure can be viewed at wileyonlinelibrary.com]

and north-east of Argentina, the positive rainfall tendencies began in the mid-1970s and may be linked to higher intensities and frequencies of the El Niño Southern Oscillation (ENSO) phenomena (Barros *et al*., 2000).

Previous climate variability analyses documented two hydrologic periods for the Paraná River basin in the 20th century: low precipitation and low river discharges between 1930s and 1970s and high precipitation as well as high river discharges from 1970s onwards (García and Vargas, 1998). Furthermore, four extraordinary floods were recorded in the Middle Paraná River in 1905, 1983, 1992 and 1997/1998, and these were associated with ENSO events (Barros *et al*., 2006). The extraordinary flood of 1983 was the most severe flood ever registered in the Paraná River (Camilloni and Barros, 2000). The water levels and maximum discharge during 1983 flood were similar to those during floods of 1992 and 1997/1998; however, the duration of this flood was extremely long, with water levels above 5 m for 12 months. Our analyses of the flood pulse variations among years identified three groups with clearly different characteristics (years with large and long floods, years with short floods and years characterized by just flow pulses and no flooding). General frequency of years with large floods increases along analysed decades with almost all years from 1980s onwards characterized by large floods.

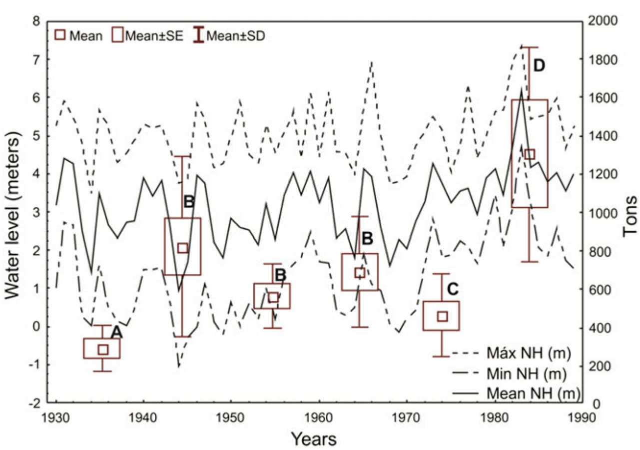

Figure 5. Mean, maximum and minimum (average) annual water levels for the period 1930–1989. Box plot with average of commercial fish catches per decade. Codes A, B, C and D express significant differences (based on permutational analysis of variance (PERMANOVA) test and pairwise a posteriori comparisons) among decades along the study period

Implications for fish populations and fisheries

The commercial catches in the Middle Paraná River were significantly higher in decades with frequent large floods (e.g. 1980s) compared with decades with infrequent flood events (e.g. 1950s). Large floods seem to enhance recruitment of commercially important fish species (Agostinho *et al*., 2004; Espínola *et al*., 2014), most of which are large migratory species extensively using floodplain as nurseries for larvae and juveniles. It was previously documented that *P. lineatus*, *L. obtusidens* and *P. albicans* use floodplain habitats as areas of reproduction and larval nurseries, while *S. brasiliensis* and *P. corruscans* only as larval nurseries (Bonetto and Pignalberi, 1964; Oldani and Oliveros, 1984; Rossi *et al*., 2007; Abrial *et al*., 2014). Strong correlations between high water levels and increased floodplain connectivity and fish abundance and diversity were also reported for the Upper Paraná River (Suzuki *et al*., 2009; Espínola *et al*., 2014). Furthermore, Agostinho *et al*. (2004) postulated that recruitment of large migratory fish species in

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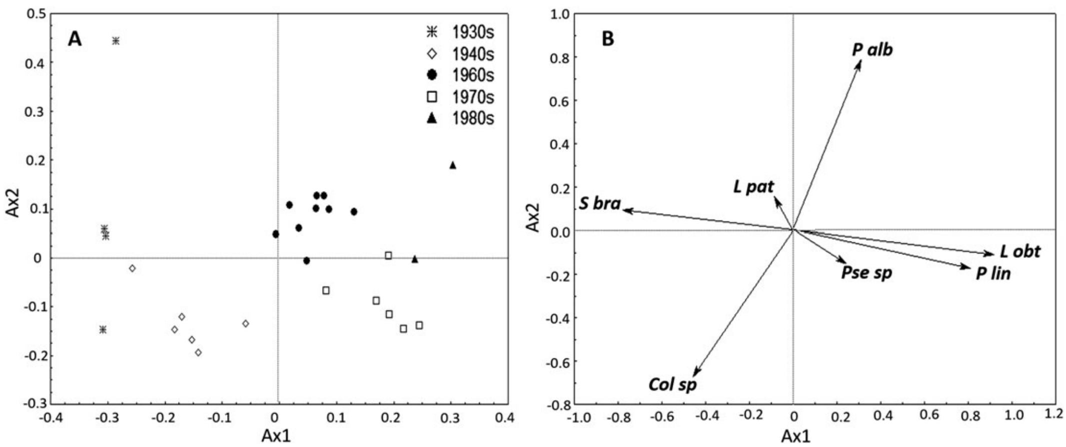

Figure 6. (A) Canonical analysis of the principal coordinates (CAP) (constrained) of temporal variation of commercial fish species structure on the Middle Paraná River during 1936–1982. Fish catches by species were not recorded in the 1950s. (B) Commercial fish species catches structured among decades along the study period

Upper Paraná River was favoured during floods longer than 75 days.

Most fish populations in the Middle Paraná River appear to strongly depend on variations in the flow regime. The long-distance migratory species analysed shown a pronounced synchronism with the hydrologic cycle and recruitment and in general produce many small eggs and do not display parental care (Agostinho *et al*., 2004, 2007). Floods play an important role in the recruitment of these species, as much by influencing spawning success as well as their effect on the survival of juveniles (Bailly *et al*., 2008). A large flooding in a particular year generally resulted in a higher fish catch 2 years later, suggesting that the abundance of catchable fish increases, probably through better juvenile recruitment during high flood (Junk *et al*., 1989; Górski, 2010). Quirós and Cuch (1989) also observed relative maxima in total catches (especially of *P. lineatus*) 2 years after a large flood event in the Middle Paraná River. Furthermore, these authors denote that the relationship between total catch and water levels are also strong with lags of 5, 6 and 7 years. This probably relates the fact that large-bodied silurids recruited in years with large floods are actually taken by the fishery 5–7 years later (Oldani and Oliveros, 1984).

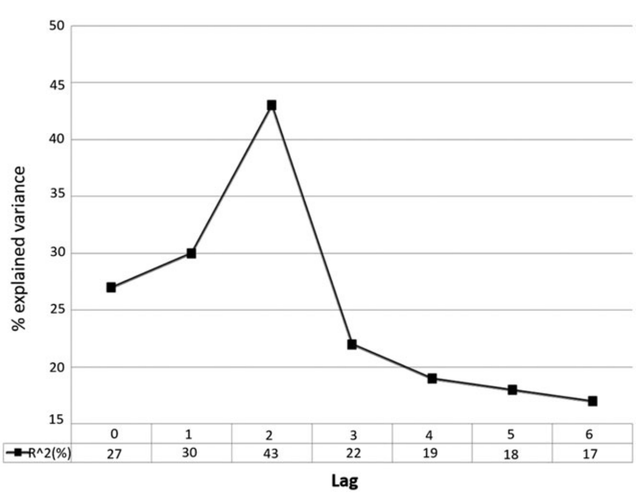

Figure 7. R^2 (%) of models from the db-RDA analysis with different lag periods (0–6 years)

The lag period in the response of fish catches to flood pulse characteristics seem to differ among river systems and relates to life-history characteristics of fish in these systems. For example, Moses (1987) reported positive correlations between fish catches and the flood indices of the previous year in the Cross River (Nigeria, Africa), but unlike in our study, the correlations were not significant considering a lag of 2 years. Our results reported for the Middle Paraná River are, however, in accordance with Welcomme (1975) who reported positive and significant correlation between the catches and the flood intensity of previous years (hydrological indices; lags 1 and 2) for the Shire (Mozambique), Niger (Malí) and Kafue (Zambia) floodplain rivers in Africa.

The inclusion of the period 1982–1984, the exceptionally high maximum and minimum hydrological levels in 82–83 highly improves the amount of variance in the catches explained by flow characteristics. This period also strongly coincided with the increase in catch of *P. lineatus* (Quirós and Cuch, 1989). *P. lineatus* is the species most directly associated with floodplains, and they often dominate commercial catches in the Middle Paraná River (Quirós and Cuch, 1989). Our results indicated that variables relating to flood magnitude and the minimal water levels along the year explained the largest proportion in the variability of fish catches. This corroborates results obtained by Quirós and Cuch (1989), who postulated that catches depended on flooding intensity and on the amount of water remaining in

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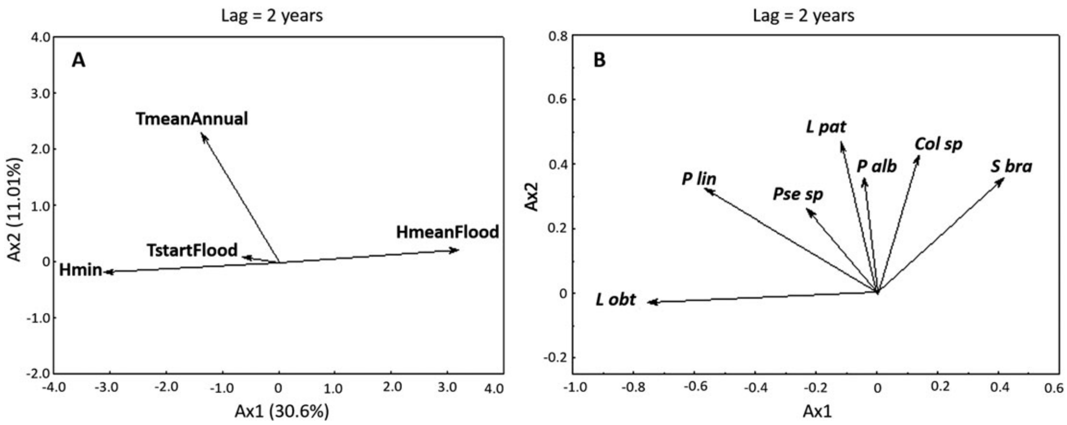

Figure 8. (A) Distance-based redundancy analysis (dbRDA) of log10-transformed fish catches in the Middle Paraná River from 1936 to 1982 explained by flow regime variables. The analyses were performed with lag 2. (B) Plot of commercial fish species catches structured by flow regime variables along the study period

the system (principal channel and floodplain) during the low-water season in the years in which the age classes taken by the fishery were born. Welcomme (1975) postulated that this is because the magnitude of high-water periods positively affects the size of stock, survival and growth of fish and the minimum water level affects negatively the natural survival and ease of catches during the low-water periods. These findings also confirm the governing role of duration and magnitude of flood pulses in recruitment success of riverine fish reported in other large river–floodplain systems (Bailly *et al*., 2008; Górski, 2010).

On the other hand, other anthropogenic factors might also influence the fluctuations of commercial fish catches, as it was observed for *S. brasiliensis*. This species decreased in catches in the 1960s and was not recorded in 1973–1975 as total ban of fishing for this species was imposed because of low levels of catches registered in previous decades (Fuentes and Quirós, 1988). The catches recovered towards the end of the 1970s and early 1980s. The marked decrease of *S. brasiliensis* as well as *Colossoma* sp. probably caused displacement of the fishing of these species towards *Pseudoplatystoma* sp. and *P. lineatus* (Fuentes and Quirós, 1988). Furthermore, other factors such as direct river engineering and construction of impoundments might have also affected the commercial fish catches in the Middle Paraná River. A total of ~40 dams have been built in the Upper Paraná River up to year 2000 (Agostinho *et al*., 2007). These dams block fish migration routes and may cause negative effects on riverine fish community in the region (Agostinho *et al*., 2008). These are located, however, about 740 km upstream from the floodplain zone of the Middle Paraná River in Argentina. It is denoted that no quantitative studies exist that evaluates their effect on migration of the fish community of this reach (Espínola *et al*., 2014). Negative effects of these dams on fish community of the Middle Paraná River seems unlikely as this reach is part of a large still free-flowing corridor of more than 1500 km that coincides with documented fish migration routes (Bonetto and Pignalberi, 1964; Baigún *et al*., 2003). Furthermore, these dams seem to have minor effects on the flow regime of the Middle Paraná River, which continues to depend mostly on climatic variability and long-term changes in the hydrologic regime (Giacosa *et al*., 2000; Paoli and Cacik, 2000).

CONCLUDING REMARKS

The climatic fluctuations during the 20th century strongly affected the hydrology of the Middle Paraná River and the characteristics of its flow regime. The magnitude of floods, as well as maximum, minimum and mean water levels increased in association with an increment of frequency and intensity of ENSO events. Floods that are a key factor driving recruitment of commercial fish species were significantly more frequent and important in the 1980s. These fluctuations were a direct cause of increased abundance and commercial catches in the 1980s because of enhanced recruitment of commercially important species. This highlights the positive influence of the duration and magnitude of floods on commercial catches of riverine fish in subtropical large river systems. Middle Paraná River remains a large, heterogeneous and unimpounded river system without notorious direct anthropogenic changes, where the hydrological regime and water quality remain in an almost pristine state. This natural flow regime must be preserved in order to maintain productive fisheries in this system.

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REFERENCES

Abrial E, Rabuffetti AP, Espínola LA, Amsler ML, Blettler MCM, Paira AR. 2014. Influence of hydrological changes on the fish community in two lotic environments of the Middle Paraná Floodplain, Argentina. *Aquatic Ecology* **48**: 337–349.

Agostinho AA, Gomes LC, Veríssimo S, Okada EK. 2004. Flood regime and fish: effects on spawning, recruitment and attributes of the assemblages in the Upper Paraná River floodplain. *Reviews in Fish Biology and Fisheries* **14**: 11–19.

Agostinho AA, Gomes LC, Pelicice FM. 2007. *Ecology and Management of Fisheries Resources in Reservoirs of Brazil*. EDUEM: Maringá.

Agostinho AA, Pelicice FM, Gomes LC. 2008. Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. *Brazilian Journal of Biology* **68**: 1119–1132.

Anderson MJ. 2001. Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 626–639.

Anderson MJ. 2004. A program for generalised discriminant analysis or canonical correlation analysis on the basis of any distance measure. Department of Statistics, University of Auckland.

Anderson MJ, Gorley RN, Clarke KR. 2008. *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. Plymouth: UK.

Baigún C, Sverlij SB, López HL. 2003. Recursos pesqueros y pesquerías del Río de la Plata interior y medio (Margen Argentina). *Informes de la División Zoología Vertebrados de la Universidad Nacional de la Plata, Argentina*.

Bailly D, Agostinho AA, Suzuki HI. 2008. Influence of the flood regime on the reproduction of fish species with different reproductive strategies in the Cuiabá River, Upper Pantanal, Brazil. *River Research and Applications* **24**: 1218–1229.

Barros V, Castañeda ME, Doyle M. 2000. *Southern Hemisphere Paleo and Neo-climates*. Springer-Verlag: Berlin, Heidleberg.

Barros V, Clarke R, Dias PS. 2006. Climate change in the La Plata Basin. Publication of the Inter-American Institute for Global Change Research (http://www.iai.int/). CIMA-CONICET-UBA, Argentina.

Bonetto AA and Pignalberi C. 1964. New contributions on fish migration in Argentinian rivers flowing through the Mesopotamia region. *Reports from the National Institute of Limnology* (*INALI*), Santo Tomé, Santa Fe, Argentina (in Spanish) **1**: 1–14.

Bonetto AA, Cordiviola de Yuan E, Pignalberi C, Oliveros O. 1969. Ciclos hidrológicos del río Paraná y las poblaciones de peces contenidas en las cuencas temporarias de su valle de inundación. *Physis* **29**: 213–223.

Camilloni E, Barros V. 2000. The Paraná River response to El Niño 1982–83 and 1997–98 events. *Journal of Hydrometeorology* **1**: 412–430.

Drago EC. 1989. Morphological and hydrological characteristics of the floodplain ponds of the Middle Paraná River (Argentina). *Revue d'Hydrobiolgie Tropicale* **22**: 183–190.

Drago EC, Amsler ML. 1988. Suspended Sediment at a Cross Section of the Middle Paraná River: Concentration, Granulometry and Influence of the Main Tributaries. Sediment Budgets (381–396). Proc. of the Porto Alegre Symposium, IAHS Publ. N° 174. ISBN 0-947571-56-6.

Espinach Ros A. 1993. Informe de la sexta reunión del grupo de trabajo sobre recursos pesqueros. *FAO. Informe de pesca N° 490*. Montevideo, Uruguay.

Espínola LA, Amsler ML, Paira AR, Drago EE, Blettler MCM, Agostinho AA. 2014. Effects of decadal changes in the hydrological regime of the middle reach of the Paraná River (Argentina) on fish densities. *Environmental Biology of Fishes* **97**: 757–771.

FAO. 2014. Perfiles de pesca y acuicultura por países. Argentina. Hojas de datos de perfiles de los países. In: *Departamento de Pesca y Acuicultura de la FAO* [online]. Roma. Actualizado 2014. [21 October 2015]. http://www.fao.org/fishery/facp/ARG/es

Fuentes CM and Quirós R. 1988. Variación de la composición de la captura de peces en el río Paraná durante el período 1941–1984. Departamento de Aguas Continentales. Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP). ISSN 0326–8659. Informe Técnico N°6. Argentina

García NO, Vargas WM. 1998. The temporal climatic variability in the Río de La Plata basin displayed by the river discharges. *Climatic Change* **38**: 359–379.

Gehrke PC, Sheaves MJ, Boseto D, Figa BS, Wani J. 2011. Vulnerability of tropical pacific fisheries and aquaculture to climate change. Chapter Secretariat of the Pacific Community, Noumea, New Caledonia. **10**: 577–645

Giacosa R, Paoli C, Cacik P. 2000. El río Paraná en su tramo medio (Capítulo 2: 69–103). Centro de Publicaciones, Universidad Nacional del Litoral, Santa Fe, Argentina.

Giorgi F. 2003. Variability and trends of sub-continental scale surface climate in the twentieth century. Part I: observations. *Climate Dynamics* **18**: 675–691.

Górski K. 2010. Floods and fish: recruitment and distribution of fish in the Volga River floodplain. Wageningen UR: Wageningen; 1–224. ISBN: 978-90-8585-815-7 http://edepot.wur.nl/154839.

Górski K, Winter HV, de Leeuw JJ, Minin AE, Nagelkerke LAJ. 2010. Fish spawning in a large temperate floodplain: the role of flooding and temperature. *Freshwater Biology* **55**: 1509–1519.

Górski K, De Leeuw JJ, Winter HV, Vekhov DA, Minin AE, Buijse AD, Nagelkerke LAJ. 2011. Fish recruitment in a large, temperate floodplain: the importance of annual flooding, temperature and habitat complexity. *Freshwater Biology* **56**: 2210–2225.

Górski K, Van den Bosch LV, Van de Wolfshaar KE, Middelkoop H, Nagelkerke LAJ, Filippov OV, Zolotarev DV, Yakovlev SV, Minin AE, Winter HV, de Leeuw JJ, Buijse AD, Verreth JAJ. 2012. Post-damming flow regime development in a large lowland river (Volga, Russian Federation): implications for floodplain inundation and fisheries. *River Research and Applications* **28**: 1121–1134. DOI:10.1002/rra.1499.

Górski K, Buijse AD, Winter HV, De Leeuw JJ, Compton TJ, Vekhov DA, Zolotarev DV, Verreth JAJ, Nagelkerke LAJ. 2013. Geomorphology and flooding shape fish distribution in a large-scale temperate floodplain. *River Research and Applications* **29**: 1226–1236. DOI:10.1002/rra.2610.

Górski K, de Leeuw JJ, Winter HV, Khoruzhaya VV, Boldyrev VS, Vekhov DA, Nagelkerke LAJ. 2016. The importance of flooded terrestrial habitats for larval fish in a semi-natural large floodplain (Volga, Russian Federation). *Inland Waters* **6**: 105–110.

Hammerly JA. 2011. La calidad del agua. In: Río Paraná: 203–214. Bolsa de Comercio de Santa Fe, Argentina. ISBN 978-987-21099-4-3.

Copyright © 2016 John Wiley & Sons, Ltd.

IPCC. 2014. Cambio climático 2014: impactos, adaptacion and vulnerabilidad. Resumen para responsables de políticas. GTII; OMM; PNUMA. Suiza.

Iriondo M, Parma MJ, Paggi JC. 2007. *The Middle Paraná River—Limnology of a Subtropical Wetland*. Springer-Verlag: Berlin Heidelberg.

Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river–floodplain systems. *Canadian Journal of Fisheries and Aquatic Sciences Special Publication* **106**: 110–127.

Latrubesse E. 2008. Patterns of anabranching channels: the ultimate end-member adjustment of mega rivers. *Geomorphology* **101**: 130–145.

Legendre P, Legendre L. 2012. *Numerical Ecology*, vol. **24**. Elsevier: Amsterdam; 265–335.

López H. 2001. Estudio y uso sustentable de la Biota Austral: ictiofauna Continental Argentina. *Revista Cubana de Investigaciones Pesqueras* (Supl. Especial, versión electrónica). SIN CUB 0138–8452.

Manly BFJ. 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology, 2nd*. Chapman & Hall: London.

McArdle BH, Anderson MJ. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* **82**: 290–297.

Moses BS. 1987. The influence of flood regime on fish catch and fish communities of the cross river floodplain ecosystem, Nigeria. *Environmental Biology of Fishes* **18**: 51–65.

Neiff JJ. 1990. Ideas para la interpretación ecológica del Paraná. *Interciencia* **15**: 424–441.

Oldani NO, Oliveros OB. 1984. Estudios limnológicos en una sección transversal del tramo medio del río Paraná. XII: dinámica temporal de peces de importancia económica. *Revista de la asociación de ciencias naturales.* **15**(2): 175–183.

Oliveira AG, Suzuki HI, Gomes LC, Agostinho AA. 2014. Interspecific variation in migratory fish recruitment in the Upper Paraná River: effects of the duration and timing of floods. *Environmental Biology of Fishes*. **98**: 1327–1337.

Paira AR. 2003. Características morfométricas de lagunas de la llanura de inundación del río Paraná Medio. Universidad Nacional del Litoral, Santa Fe, Argentina, *Tesis de Licenciatura en Cartografía*

Paoli C and Cacik P. 2000. *The Paraná River in its middle reach*. Contribution to science and engineering practices in a large lowland river. Centro de Publicaciones. Universidad Nacional del Litoral. Santa Fe. Argentina **1**: 105–171.

Quirós R, Cuch S. 1989. The fisheries and limnology of the lower Plata River Basin. *Canadian Journal of Fisheries and Aquatic Sciences* **106**: 429–443.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org

Rossi L, Cordiviola E, Parma MJ. 2007. *The Middle Paraná River. Limnology of a Subtropical Wetland*. Springer-Verlag: Heidelberg, Germany.

Suzuki HI, Agostinho AA, Bailly D, Gimenes MF, Julio JHF, Gomes LC. 2009. Inter-annual variations in the abundance of young-of-the-year of migratory species in the Upper Paraná River floodplain: relations with hydrographic attributes. *Brazilian Journal of Biology* **69**: 649–660.

Sverlij S, Espinach Ros A. 1986. El dorado, *Salminus maxillosus* (Pisces, Characiformes) en el Río de la Plata y Río Uruguay inferior. *Revista de Investigación y Desarrollo Pesquero* **6**: 57–75.

Tockner K, Malard F, Ward JV. 2000. An extension of the flood pulse concept. *Hydrological Processes* **14**: 2861–2883.

Ward JH. 1963. Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association* **58**: 236–244.

Welcomme RL. 1975. The fisheries ecology of African floodplains. CIPA Technical Paper **3**: 1–51.

Welcomme RL. 1985. River fisheries. . FAO Fish Technical Paper ISBN 92-5-302299-X

Winemiller KO. 2004. Floodplain river food webs: generalizations and implication for fisheries management. Proceedings of the second international symposium on the management of large rivers for fisheries. FAO Office for Asia and the Pacific, Bangkok.

Wu N, Górski K, Daniel AJ. 2013. Abundance of larval native and nonnative fishes in floodplain habitats of the lower Waikato River, New Zealand. *Inland Waters* **3**: 359–368.

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