Commercial fisheries in a mega unregulated floodplain river: assessment of the most favourable hydrological conditions for its preservation

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Funding information

This study was funded by Agencia Nacional de Promoción Científica y Técnica (PICT N°1855 2013–2015 and PIP Project N°438 2014–2016) of Argentina and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina).

ABSTRACT

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/jfb.14184

This paper deals with the hydrological variability effects on the primary commercial fish species inhabiting the main channel and the floodplain of the large Paraná River in its middle reaches in Argentina. Analysing more than eight decades (1935–2016) of information on the most frequent and abundant commercial species in conjunction with hydrological levels and temperature, our results show that spring–summer floods of a certain magnitude (*c.* 6 m) and durations (> 80 days) are crucial for sustaining commercial fisheries. Moreover, the frequency of these floods was modulated by the decadal climatic fluctuations that have occurred over the past 100 years in the Paraná Basin. An insight into the probable incidence of some anthropogenic influences is also provided.

KEYWORDS

inland fisheries, hydroclimatic variability, middle Paraná River, reproductive success

1 | INTRODUCTION

Hydrological fluctuations with alternating low-water and high-water phases govern the degree of lateral connections in floodplain rivers and facilitate the exchange of water, nutrients and organisms among the main channels and the adjacent floodplain (Junk *et al.*, 1989; Lowe McConnell, 1987; Neiff, 1990; Thomaz *et al.*, 2004). These hydrological variations and water temperature are considered the principal driving forces of functioning and structuring in freshwater ecosystems (Poff and Ward, 1989; Tockner e*t al.*, 2000; Thomaz *et al.*, 2004). Specifically, seasonal flooding in phase with warm temperatures during spring-summer is considered to be the key environmental factor that drives the structuring of communities and the distribution of aquatic organisms in floodplains (Junk *et al*., 1989; King *et al*., 2003; Thomaz *et al*., 2004).

Periodical inundations are crucial for important ecological attributes of fish assemblages (*e.g*., interactions, feeding, reproduction and recruitment) and sustain diversity and productivity of floodplain rivers (Agostinho *et al*., 2004; Górski *et al*., 2011; Humphries *et al*., 2014; Junk *et al*., 1989; King *et al*., 2003). Indeed, several migratory Neotropical fishes species are characterised by a high degree of synchronization between their reproductive cycle and the seasonal river flow dynamics (Agostinho *et al*., 2004, 2007; Bailly *et al.*, 2008; Winemiller, 2004). That link between commercial fish stocks and natural pulse dynamics was suggested by Bonetto and Pignalberi (1964), Godoy (1975) and Moses (1987).

While temperature is a crucial variable for fish structuring, its variations are minimal or fairly regular if compared with hydrological fluctuations in subtropical and tropical floodplain rivers; thus the river regime and periodic flooding become the associated primary drivers which modulate the dynamics of migratory fish populations (Junk *et al*., 1989; Humphries *et al*., 2014; Winemiller, 2004). Attributes of flood pulses such as their duration, magnitude and timing as well as the characteristics of low-water phases are main factors that control the connectivity of floodplains that modify the availability of habitats that riverine fish utilise as natural nurseries for spawning and growth (Agostinho *et al*., 2007; Baigún *et al*., 2003; Górski *et al*., 2013; Quirós, 1990). Winemiller (2004) shows that increased connectivity prompts larger species diversity.

Several studies dealt with the values of inundation attributes which optimise the reproductive success and recruitment of inland commercial fisheries in floodplain river systems (Agostinho *et al*., 2004; Górski *et al*., 2011; King *et al*., 2003; Welcomme and Halls, 2004). Estimation of timing, magnitude and duration of the most favourable floods (Fernandes *et al.,* 2009) was always focused on the upper basin of Paraná River, showing that floods longer than 75 days and intensities higher than 6.1 m have significantly enhanced reproduction and recruitment of fish assemblages (Agostinho *et al*., 2004; Suzuki *et al.,* 2009). There are no similar quantitative studies for the lower basin which includes the middle reaches of the Paraná River. Even though the effects of floods on fish structure are widely addressed, most research works are based on short-term records (Abrial *et al*., 2014; Espínola *et al.*, 2014; Rossi *et al.*, 2007; Scarabotti *et al*., 2011).

The largest freshwater fisheries in Argentina are located along the middle reaches of the Paraná River and comprise almost the entire continental fishing production of the country (Baigún *et al*., 2003, 2013), estimated at 15,000 t year^{-1}1925–1987 (Espinach Ros, 1993). These resources generate important incomes estimated at US $113 million of revenue from exports in the period from 2007 to 2013 and they are also a substantial fraction of dietary proteins for many people in the region (FAO, 2014). Most commercial fish, *c.* 20 species, are large and perform periodic and large breeding migrations [*e.g.*, *Prochilodus lineatus* (Valenciennes 1837), *Salminus brasiliensis* (Cuvier 1816), *Megaleporinus obtusidens* (Valenciennes 1837), Bonetto and Pignalberi (1964); Fuentes and Quirós (1988)], taking advantage of spring–summer floods (Abrial *et al.,* 2018). Breeding occurs in the main channels whereas the different floodplain lentic habitats are used as nursery areas for larvae and juveniles (Baigún *et al*., 2003). It is therefore postulated that connectivity variations in the floodplain modulated by the changing hydrology are crucial for the completion of life cycles (Quirós, 1990).

Through the analysis of the hydrological variability recorded over more than 100 years in the middle Paraná River, this paper focuses on analysing and quantifying the most favourable flood pulse attributes (*e.g*., magnitude, duration, timing) for the reproductive success of the main commercial fish species. In this sense, the main goal is to establish the best flooding characteristics for fisheries conservation so as to assure favourable effects for recruitment and survival. Fish databases from several sources, which span nearly eight decades, are used in the analysis. We also considered the effects of decadal climate cycles on the basin's hydrology and the probable incidence of anthropogenic impacts on these results.

1 | MATERIALS AND METHODS

All protocols for fish capture and handling were approved by the Ethics and Safety Board of the Faculty of Biochemistry and Biological Sciences of Universidad Nacional del Litoral (Santa Fe, Argentina).

2.1 | Study area

The Paraná River is the second largest river in South America, one of the mega-rivers of the world (Latrubesse, 2008). The studied area extends along the Paraná River and its floodplain between 27° and 32° S and from 58° to 60°W, from the confluence of the Paraná River with its main tributary, the Paraguay River, to Diamante city (Figure 1). In the upper limit of the studied area, the Paraná River has a discharge of approximately 17000 $m^3 s^{-1}$, which is caused by the confluence of the upper Paraná River (*c.* 12400 $m^3 s^{-1}$) and the Paraguay River (*c.* 3800 $m^3 s^{-1}$). The Paraná River in its middle reaches (from now on referred to as the middle Paraná River) is characterised by the strong presence of highly productive *Potamon* crab species and an extensive and complex adjacent floodplain with numerous secondary channels, lakes and swamps (Latrubesse, 2008). Its alluvial plain extends mostly along the western bank of the main river channel and covers an area of *c.* 13000 km^2 (Drago, 1989). Unlike the upper Paraná in Brazil, where numerous large dams have been built since the end of the 1960s [*c.* 40 before 2000 (Agostinho *et al.*, 2008) but now more than 100 (Lehner *et al.,* 2011)], the middle Paraná River remains unimpounded. Dams could have contributed to increasing the mean annual discharge by preventing very low water levels (Anderson *et al.*, 1993), since they can release water from their reservoirs during dry periods (Antico *et al.*, 2018). The most direct effect observed on the hydrograph of the middle Paraná River is the increase in minimum water levels (Quiros, 1990).

The middle reaches are situated in a moderate humid subtropical-temperate climate. Mean annual temperature is *c.* 19.25 ºC. Annual precipitation is *c.* 900 mm, rains being recorded mainly from October to April (73%; Paoli & Cacik, 2000). The natural flow regime of the Paraná River has high and low water-level seasons: intensive rains in the upper basin produce floods in phase with the warm period in summer–autumn (December–April), while early spring (September–October) is characterised by a low-water period (Giacosa *et al.*, 2000). Such hydrological conditions generate a successful reproduction, recruitment and growth of commercial fish in the whole basin (Abrial *et al.*, 2014; Agostinho *et al.*, 2004, 2007; Espínola *et al.*, 2016; Suzuki et al., 2009).

2.2 | Commercial fish data

We analysed data that belong to the middle Paraná River (Figure 1), which houses the major concentration of Argentine freshwater fisheries (Fuentes & Quirós, 1988). The data on commercially important fish in the middle Paraná River for 1935–2016) were obtained from: (1) Ministerio de Agricultura de Argentina (Ministry of Agriculture of Argentina), Dirección Nacional de Pesca (the Argentine directorate of inland fisheries): generated the historical set of official statistics (commercial catches) of Producción Pesquera Argentina (the Argentine inland fishery production, PPARG, 1935–1983). (2) Ministerio de Producción (Ministry of Production), Subdirección General de Ecología de Santa Fe (Sub-directorate General of Ecology of Santa Fe Province): provided a data set of fiscal fishing (commercial catches) records (PPSF, 2011–2015). (3) Instituto Nacional de Limnología (the Argentine Institute of Limnology (INALI), which is part of Consejo Nacional de Investigaciones Científicas y Técnicas de Argentina (the Argentine Scientific and Technical Research Council; CONICET): generated data on different fish attributes (total length L_T, cm; standard length L_S, cm; total mass M_T, g), collected in lotic and lentic environments of the floodplain (INALI, 1964–1996). (4) Laboratorio de Hidroecología (Laboratory of Hydroecology, LH, which is part of INALI): collected records of fish fauna (L_T, L_S and M_T) from lotic–lentic environments of a particular section of the floodplain (LH, 2009–2016).

The different sets form a long-term series of > 50 years of information on commercial fish species. The largest gaps are concentrated in the 1950s and in the period between 1997 and 2008. The landing ports used in the analysis were selected according to their representativeness of the middle Paraná River and the completeness of the data recorded in each period (1935–1983, 2011–2015). The applied methodology was described by Rabuffetti *et al.* (2016).

PPARG began keeping records *c.* 1930s and they have been updated with sufficient completeness and quality for nearly 50 years. The data consist of landing reports of annual catches (total and by species) recorded by Prefectura Naval Argentina (*Naval Prefecture of Argentina*) in ports along the Paraná River (Figure 1). Commercial catches were recorded by species in tonnes for each port along the fluvial corridor (Fuentes & Quirós, 1988). A similar data collection system was applied for the PPSF set, but it was performed by the Ministry of Production of Santa Fe Province. Unfortunately, no information on exact fishing efforts was available in commercial datasets. The values recorded in both datasets do not include catches by sport and artisanal fishers who do not hold a fishing licence (Baigún *et al*., 2003; Espinach Ros *et al*., 2012).

We determined the method and effort for fish sampling applied in peer-reviewed articles based on the INALI dataset, all being performed by different research groups at INALI from the 1960s to the 1990s (1964–1969, 1971–1973, 1978–1980, 1984–1996; Cordiviola de Yuan, 1980; Oldani & Oliveros, 1984). The most common and frequently applied method was the trammel net. Fish information considered in this analysis was collected from multiple lentic and lotic environments of the floodplain area near Santa Fe city (Figure 1).

The fish collection in the LH set was built up from 2009 to 2016 (2 or 3 times per year). We standardised effort, sampling frequency and fishing gear. Gillnets of different mesh sizes (3 to 16 cm between opposite knots) were used for fish capture. They were laid for a 24 h period and checked every 8 h in 4 lotic and 2 lentic habitats. Caught fish were anaesthetised using 5% benzocaine and sacrificed. Specimens that were representative of the local fauna were deposited in the scientific collection at Laboratorio de Hidroecología (LH; INALI-CONICET). All specimens were identified to species level (Almirón *et al*., 2015) and common biometric data were processed on site (L_T, cm; L_S, cm; M_T, g).

The contribution made by the different fish species to the total catch in each selected site and port per dataset was assessed by calculating the ratio (%) per species and per year for each site and port. In commercial datasets, subsequently, the calculated percentages per species were arcsine-transformed. The most abundant and frequent species that were common to the different datasets that appear throughout the analysed period were selected (Table 1). These selected fish species accounted for *c.* 75% of commercial catches in the middle Paraná River. Since each database applies different effort and sampling methods, we analysed each of them in isolation.

2.3 | Hydroclimatic data

Daily water levels of the Paraná River at the Santa Fe Port's gauge Station (Figure 1) over the studied period (1905–2016) were supplied by Naval Prefecture of Argentina. Daily air temperature (T_A) for the studied period was obtained from Servicio Metereológico Nacional (National meteorological service of Argentina) in Santa Fe city (1920–2016). Since daily records of water temperature (T_W) are not available, considering T_A they were estimated through the method proposed by Drago (1984) for a section of this same studied area. T_W was calculated as follows: $T_W = 0.47 + 0.95\ T_{A15}$, where: T_{A15} is the average of T_A for the 15 day period before the considered date. This method considered that T_W is largely dependent on T_A with a slight delay.

The reference level for variable analysis of the hydrological regime within the studied area was set at 4.50 m, this being the level at which water begins to flood the adjacent floodplain (overflow level, flood pulses) and thus increases connectivity (Abrial *et al.,* 2018). A 2.3 m height was selected as the reference for disconnection of most lakes in the floodplain (Drago, 1980; Abrial *et al*., 2018). Between floods and low water periods, high water level periods occur below the bank overflow (high magnitude variations of the levels within channel banks). These fluctuations are referred to as flow pulses by Tockner *et al*., (2000). In the present study, the limits of flow pulses (FP) were considered as hydrological variations below 4.5 m and over 3.2 m (L. A. Espínola, unpubl. data).

2.4 | Long-term data analysis: flow regime and fish catches

To analyse variations in the river's flow regime in the studied period (1920–2016), we applied 18 relevant hydrological variables obtained from the daily data records of water and temperature that were described in the methodology presented by Rabuffetti *et al.* (2016). In order to build and compare flow typology among years over time, we conducted a cluster analysis (Ward method, Ward´s algorithm; Ward, 1963). Secondly, considering only years with floods, we quantitatively described different attributes per year, considering: magnitude (H_{max}, 4.5–7.72 m), duration (among 6–461 days > 4.5 m) and timing (delay; DateStartFlood). Moreover, we characterised inundations considering seasonality (DateStartFlood and DateH_{max}) and thus they were classified as follows: SSF, spring–summer floods (21 September–20 March); AF, autumn floods (21March–20 June); WF, winter floods (21 June–20 September); EE, extraordinary events (considering floods with H_{max} > 7m; Antico *et al*., 2014).

To analyse differences in number of days with high water level (> 4.5m) between humid-dry periods over time (1905–1930s, 1940–1960s, 1970–1990s; Camilloni *et al*., 2013), we performed a non-parametric analysis of variance (Kruskal-Wallis' test), since assumptions of homoscedasticity and normality were not verified. We then determined the number and frequency of SSF throughout the studied period (1905–2016) under different hydroclimatic scenarios (humid and dry periods, group of decades). Finally, Duration and H_{max} of floods were identified in a correlated way over time, highlighting SSFs and considering only years with biological information to identify different possible periods of study with variable hydrological conditions.

With the aim of identifying and analysing the relationship between the main hydroclimatic variables and variation of fish commercial assemblage structure, we carried out a distance-based redundancy analysis (dbRDA), a semi-parametric analysis that does not assume normality or homogeneity of variance and is performed using R package vegan (Oksanen *et al.*, 2017). These were conducted considering the most frequent and abundant species per dataset (Table 1). Forward-stepping selection procedure was applied to select the principal hydroclimatic variables on the final matrix. In addition, adjusted R^2 and variance inflation factors (VIF) were tested as selection criteria to provide the most significant variables in each model. To avoid multicollinearity, significant collinear relationships were identified between predictor variables (Pearson's $r > 0.6$) and redundant predictor variables were omitted.

To evaluate variations of catches over time, we analysed temporal fluctuations (interannual and interdecadal) of the most frequent and abundant species: the characid *P. lineatus*. This is the one of the most representative species of the assemblage (Rossi *et al.*, 2007), which has a key role in Santa Fe and Entre Ríos provinces (Del Barco, 2000) for two reasons: most anthropogenic activities are focused on that species and it is basic in the food web. In addition, it was present throughout the studied period, as shown by numerous records in all data series (1935–2016). By considering the type and quality of data (L_T, L_S) contained in our set (LH, 2009–2016), catches of *P. lineatus* were divided into two size ranges according to the different life stages of the species (young individuals, corresponding to juvenile < 25 cm L_S and pre-adults and adults >25 cm L_S). The distinction arises to consider the range of sizes of individuals of each species at first maturation (between 25–30 cm L_S;

Espinach Ross *et al.*, 2012; Rossi *et al.*, 2007). Differences in *P. lineatus* catches among decades and years were tested using a non-parametric analysis of variance (Kruskal-Wallis test) for each dataset in isolation, since assumptions of homoscedasticity and normality were not verified. Temporal variation of catches (biomass of *P. lineatus*) was plotted year by year and between decades since it was intended to examine temporal fluctuation in detail.

2.5 | Short-term data analysis: fish abundance and size structure

The effects of diverse hydroclimatic scenarios characterised by noticeable hydrological differences (1965–1967, 1978–1980, 1983–1985, 1992–1994 of INALI set and 2009–2011, 2013–2015 of LH set) on size structure of commercial fish were analysed for the studied period. These analyses were performed using the L_S range (cm) of the most frequent and abundant species of all landed and measured (LM; Table 1). To evaluate temporal variations in size structure we estimated the number of individuals (total and per species) by using 10 cm length groups. From the analysis of size structure by species, it was possible to specify the size ranges belonging to individuals of the new cohort of each hydroclimatic period (Espinach Ross *et al*., 2012; Rossi *et al*., 2007; Sverlij & Espinach Ross, 1986). Subsequently, we performed principal component analysis (PCA) to identify relationships between fish sizes (L_S) and main hydroclimatic variables. According to the Kaiser-Guttman criterion (Jackson, 1993), only axes with eigenvalues >1 were retained for interpretation.

In cluster analysis and dbRDA, differences were tested according to the Bray-Curtis dissimilarity index (Bray and Curtis, 1957); and probability values were obtained for predictor variables by means of 999 random permutations without restrictions (Manly, 1997). Analyses were carried out using R statistical software (R Development Core Team, 2014). Significance was determined at $P < 0.05$ in all analyses.

3 | RESULTS

3.1 | Hydroclimatic features: floods

Cluster analysis of the flow regime 1920–2016 resulted in four groups (Figure 2). Group 1 (33 years) mostly includes years without floods and all recorded FP with predominance of dry days. Group 2 (17 years; 7 SSF) consists in years with flood pulses of brief duration (between 10 and 87 days) and moderate magnitude. Group 3 (20 years; 7 SSF) is presented as an intermediate category between 2 and 4. Group 4 (27 years; 15 SSF) contains the biggest flood pulses with maximum magnitude (between 5.22 and 7.43 m) and long duration (between 82 to 365 days).

There were larger and more frequent inundations (group 2, 3 and 4; Figure 2 and Supporting Information Table S1) in the 1980s and 1990s, which were exceptionally humid decades with higher rates of flooding and differed from all other decades analysed and characterised by floods every year. EE increased in these periods (years linked in group 4): 1982–1983, 1992–1993 and 1997–1998, when water levels peaked up to 7.35, 7.43 and 7.26 m, respectively (in July, June and May; high degrees of connectivity; Supporting Information Table S1). The inclusion of floods recorded between 1905 and 1920 in Supporting

Information Table S1, which were not considered in cluster analyses because temperature is not available, shows that the occurrence of floods (numbers of days at high water level: > 4.5m) was higher (the statistical result is very close to the significance limit adopted in this study, $F = 3.63$, $P > 0.05$) during humid periods from 1905 to the 1930s (24 years, 2053 days) and from 1970 to the 1990s (24 years, 3126 days; $P < 0.05$) in contrast to the dry period of the past century (1940–1960s, 16 years, 1618 days).

Of the total floods recorded during the studied period (1905–2016), 29 SSF were identified (Figure 2 and Supporting Information Table S1). Of these, 9 occurred from 1920 to 1940 and one FP that exceeded 4 m was recorded in summer (1937). Between 1941 and 1970, only 3 SSFs were recorded, all of them being characterised by large duration and magnitude (linked in Group 4). In addition, one FP nearby the overflow level was recorded in summer of 1969. Then, 13 SSFs were recorded during the period between 1971 and 2000, most of them being characterised by long duration and great magnitude and two highly intense FPs in summer (1975, 1978). After that, between 2001 and 2016, 4 SSFs were recorded, two of them with high intensity (> 6m) and more than 170 days of high water levels (>4.5m).

This analysis determined an average recurrence frequency of SSFs over time of *c.* one each 3 years, only 1 being registered during dry decades and 4–6 during humid decades (Supporting Information Table S1). Furthermore, of these SSFs only 15 had a duration greater than 82 days with high water levels; and only 12 of those recorded values of great magnitude ($H_{\max}$ >6 m). These were mostly recorded within Group 4 (Figure 2). On the other hand, it is noted that years like 2010 and 1959, characterised by similar SSFs as regards magnitude ($H_{\max}$ 6.12 and 6.02 m) and duration (160 and 194 days), resulted markedly linked in cluster analysis. Finally, correlations between maximum intensity ($H_{\max}$) and Duration of each flood event over time were positively significant ($P < 0.001$) and show that SSFs had a duration of 26 to 248, with a mean of 80 days (Figure 3a). In the correlation considering only years with biological information on fish, it is noted that they coincide with SSF events of different characteristics in 17 instances (Figure 3b), while other years record information after SSFs.

3.2 | Long-term variations in fish catches

The ordination by dbRDA models for each dataset is shown in Figure 4. These are the most important hydroclimatic variables that drive and explain significant variations in fish catches of commercial assemblages over time. In each model, both retained axes were significant. The PPARG model explained 47% ($P < 0.05$) of the total variance in commercial catches; axis 1 was strongly correlated with water level ($H_{\min}$), timing (DateStartFlood) and duration of floods. Variables related to water temperature and dry periods (DryDays) were negatively correlated with axis 2. The PPSF final model accounted for 82% ($P < 0.05$) of the variance in commercial fish catches. Axis 1 was strongly correlated with duration of floods and humid periods (WetDays), whereas timing of floods (DateStartFlood) had a strong positive correlation with axis 2. These results revealed that the structuring of commercial catches, their short-term increments or reductions, was closely related to fluctuations of hydroclimatic variables that describe water levels, duration and occurrence (timing, date of start) of floods.

The highest catches of most species occurred in years following great floods (in magnitude and duration), mostly after SSFs (*e.g.*, in 1941-43, 1980-81). This effect was stronger for *Pseudoplatystoma* spp., *Pimelodus maculatus* Lacépède 1803, *Prochilodus lineatus* and *Luciopimelodus pati* (Valenciennes 1835). Quite the opposite, the lowest catches were recorded in years without floods, characterised by low degrees of connectivity, as in 2012, or in extended disconnection periods (*e.g.*, in 1944).

As regards the structuring of the main commercial species biomass in the data sets generated from fieldwork (non-commercial catches) for scientific purposes, the INALI final model shows that axis 1 was strongly and positively correlated with magnitude ($H_{\max}$), timing (DateStartFlood) and duration of floods and negatively with dry periods (DryDays). TmeanAnnual was positively correlated with axis 2. The final model of LH set explained 68% ($P < 0.05$) of the total variance in fish catches. Axis 1 was negatively correlated with DryDays and positively with $H_{\max}$ of floods, while axis 2 was correlated with delay of floods events. Fish structure was positively determined by the variables that describe magnitude and timing of flood occurrence. The highest catches were recorded after the discharge of highly intensive and early floods in spring-summer (*e.g.*, in 1984 and after the SSF of 2010). This effect was stronger for *P. lineatus* and *Megaleporinus obtusidens* (Valenciennes 1837). Meanwhile, a delay in the beginning of floods (*e.g.*, AF or WF as in 2011, 2013–2014) resulted in lowest catches. It is worth noting that in both cases the effect produced by floods on fish assemblages may be not clearly reflected in catches, since although the biomass may not increase significantly, there is an increase in abundance (catches) of juveniles. This effect was particularly strong for *P. lineatus* in 2010 and 2015 associated with SSFs.

Temporal fluctuations of *P. lineatus* catches over time are shown in Figure 5. PPARG and INALI revealed significant differences among decades ($F = 14.373$, $P < 0.01$ and $F = 15.808$, $P < 0.001$, respectively; Figure 5a,b). In both sets, the largest mean abundance was obtained in the 1980s (Figure 5a). In addition, LH set presented significant differences among years over time, considering catches of both juveniles and adults ($F = 16.366$, $P < 0.001$ and $F = 3.9391$, $P < 0.05$, respectively; Figure 5d). Although PPSFs did not present statistically significant temporal change in commercial catches, major increases were recorded in 2015 (Figure 5c).

High commercial catches were recorded in the early 1940s and 4 decreased markedly after 1944. A high increase in catches was recorded in 1964 and then in 1968–1969 during dry years (without floods; Figure 5c), in both cases after SSFs of high intensity ($H_{\text{max}} > 6$ m) and Duration (> 150 days) recorded in 1959 and 1966 (Supporting Information Table S1). In the 1980s, catches increased significantly, the highest values being recorded in 1984, after the EE in 1982–1983 (Figure 5d). In the period between 2009 and 2016, a highly significant increase in catches of juveniles occurred in 2010 ($P < 0.001$, with respect to the remaining years; Figure 5d) after the large SSF of high intensity ($H_{\text{max}} > 6$ m) and duration (> 190 days; Supporting Information Table S1). In 2016, after the SSF of greater intensity ($H_{\text{max}} > 6.6$ m) and duration (173 days), a lower increase in catches of juveniles was observed as compared with those in 2010 (Figure 5d). Larger sizes of *P. lineatus* began dominating numbers and biomass after 2012 in the floodplain, with a clear rise in 2015 (LH set), coinciding with the maximum values recorded for fiscal fishing (PPSF, commercial catches; Figure 5c).

3.3 | Hydroclimatic conditions and fish size structure

A representative view of the temporal variation of hydrology and temperature under distinct hydroclimatic scenarios and their effects on abundance and size of fish caught in the floodplain over time can be seen in Figure 6. After the largest SSF of high intensity and duration (1965–1966 and 2009–2010), abundance increased, particularly of small-sized individuals (juvenile, < 20 cm L_S) were reported mostly in 2010. In addition, when SSFs (*e.g*., in 1979–1980, 1993 and 1994) had brief duration (between 28–66 days) and reached low intensity (H_{max} between 4.82 and 5.22 m), the smaller size range was not significant and total abundance of LM species was lower. The abundant captures of larger-sized fish (> 30 cm L_S) in 1978–1979 may be related to the large SSF recorded in 1977 (Supporting Information Table S1).

When WF events were registered (*e.g*., the EE of 1992 and in the period between 2013 and 2015) or during an AF of low duration (*e.g*., 2011), there was an increase in the abundance of larger-sized fish (mostly those ranging from 30 to 60 cm L_S) in the alluvial plain and total catches diminished. After these scenarios occurred, the size range of juveniles showed little significance. In addition, after the EE of 1982–1983, individuals that were 20 to 40 cm long were generally observed and their total abundance increased markedly, which may be related to the hydrological conditions of previous years. On the other hand, in 1967 the abundance of small-sized individuals (< 20 cm L_S) was quite similar to that during and after the great SSF of 1965–1966 (Figure 6 and Supporting Information Table S1) with differences per species (a reverse trend in the case of *M. obtusidens*).

The patterns and associations of the different hydroclimatic scenarios with fish size ranges seen in Figure 7 complement those shown in Figure 6. In each case, both axes of the PCA were significant ($P < 0.05$) and retained for interpretation (66.6% and 75.8% of total variance, respectively). Mainly juveniles of LM (< 20 cm L_S) were observed after large SSFs (1965–1966, 2009–2010). Moreover, small sizes (1–10 cm L_S) were recorded in 2011 (AF, slightly significant abundance) and abundance was recorded at the beginning of the SSF of 2009. After EEs (1982–83 and 1992; Figure 7a), individuals of a larger size (corresponding to pre-adults) were recorded, which was associated with previous conditions. Larger-sized fish, mostly those ranging from 30 to 60 cm L_S, were related either to years without floods (1978–1979, after the great SSF) or to the occurrence of WF (2013 and 2014). Smaller sizes corresponding to juveniles of LM were mostly linked with variables H_{max} (> 6 m), Duration (> 150 days) and TStartFlood (timing, beginning in early summer). The correlation between years with WF (2013–2015) characterised by fish of large size related to the variable delay is shown in Figure 7b.

4 | DISCUSSION

4.1 | Long-term hydroclimatic variability

Flow regime and temperature varied substantially between 1905 and 2016 in the middle Paraná River due to hydroclimatic changes recorded in the La Plata Basin. Flood pulses were significantly more frequent between 1905 and the 1930s and between 1970 and the 1990s, with flood events taking place mostly in years between 1980 and the 1990s. Furthermore, the largest SSFs and the four EE recorded in the past 130 years occurred in these periods. This variability in flood frequency and characteristics was linked with higher intensities and frequencies of the ENSO phenomenon (Barros *et al*., 2000, 2006; Camilloni *et al*., 2013), a tendency that is associated with fluctuations of sea surface temperature (SST) and is increased with climate change (Antico *et al*., 2014; Herbert & Dixon, 2002; IPCC, 2014). The region encompassing the north-east of Argentina and the south of Brazil had the highest increase in annual precipitation during the 20th Century due to a progressive increase in temperature since the 1970s (Barros, 2013; Giorgi, 2003).

Our results and previous climate variability analyses documented for the Paraná River basin (Antico *et al*., 2014; Barros *et al*., 2000, 2006; Camilloni *et al*., 2013; García & Vargas, 1998; Giorgi, 2003) demonstrated the existence of distinct hydroclimatic periods (Figure 8): two humid periods (1905–1940 and 1970–2000) characterised by high precipitation and river discharges, frequent SSFs, more than three per decade, mostly of large intensity and duration ($H_{\max} > 6$m, duration > 80 days), and EE (years related to group 4; Figure 2); also, one dry period (1941–1960s; most years classified into group 1; Figure 2) characterised by lower precipitation and river discharges, in which the six most pronounced disconnection periods of the century were recorded and in which only 1 SSF was recorded per decade. Finally, it remains to be defined which type of period the beginning of the 21st century belongs to, considering that it involved firstly a dry decade (years mostly classified into group 1; Figure 2) followed by an apparently humid decade with two intense SSFs (Supporting Information Table S1). The results reveal that for the Paraná River basin, there is still no empirical evidence that confirms the intensification of floods caused by climate changes (IPCC, 2014), nor that the trend started in the 1970s, with the associated hydroclimatic conditions, has been reversed.

4.2 | Floods and interannual fish changes

Floods characteristics (H_{max}, duration, delay) and frequency fluctuated significantly in association with changes of hydroclimatic periods, determining interannual variability in recruitment and catches of commercial fish in the middle Paraná River. During humid decades (*e.g.*, 1980s), catches were significantly higher, decreasing markedly in dry decades such as that recorded in the middle of the past century (*e.g.*, mid 1940s–1960s; Rabuffetti *et al.*, 2016). The adverse conditions recorded in the floodplain during dry scenarios, with the non-occurrence of SSFs and the longest disconnection periods have caused negative effects on reproduction, larval abundance (Fuentes and Quirós, 1988), available nursery areas and recruitment (Abrial *et al*., 2014; Agostinho *et al*., 2004; Scarabotti *et al*., 2017), especially for LM juveniles (Figures 5, 7). In contrast, increments in catches of *P. lineatus* in humid scenarios (*e.g*., 1980s, 1990s; Figure 4) may be explained by an increase in the dispersal opportunity of adult individuals (Agostinho *et al*., 2004; 2007; Oliveira *et al*., 2014; Scarabotti *et al*., 2017) due to greater availability of habitats in the alluvial plain caused by the high connectivity generated in the system under extremely wet conditions. In addition, high commercial catches recorded in the early 1940s may be the result of the beneficial hydroclimatic conditions of the previous humid decade characterised by frequent SSFs.

Commercial fish that make an extensive use of floodplains either as nurseries for larvae and juveniles or as habitat for feeding and reproduction (*e.g.*, *P. lineatus*, *M. obtusidens and* the catfish *P. maculatus*; Abrial *et al*., 2014; Bonetto & Pignalberi, 1964; Espínola *et al*., 2016; Rossi *et al*., 2007) were positively influenced by the beneficial hydroclimatic conditions recorded in humid scenarios. After SSFs of a certain magnitude and durations (*e.g.*, 1940, 1959, 1966, 1977, 2010; Figure 8), both fish abundance and catch of juveniles were significantly increased in strong correlation with magnitude ($H_{\max}$), duration and timing of floods (Figures 6, 7). Fish recruitment positively benefited from these characteristics of the attributes and frequency of floods. King *et al.* (2003) postulated that optimum flood conditions for success in fish recruitment must coincide with high temperature, duration (lasting from several weeks to a few months) and cover an extensive floodplain area. This synchronisation between high water levels, increased floodplain connectivity, temperature and fish abundance has also been reported in other floodplain river systems (Agostinho *et al*., 2004; Górsky *et al*., 2013; Moses, 1987; Welcomme, 1975). Smederevac-Lalić *et al.* (2017) have recently postulated a very similar pattern of positive correlations for the Danube River, with timing, duration and magnitude of floods and negative correlations with number of dry days, thus significantly affecting interannual fluctuations of commercial fisheries.

It was postulated that recruitment of LM fish species in upper Paraná River was favoured by floods longer than 75 days (Agostinho *et al*., 2004) and intensities higher than 6.1 m (Suzuki *et al*., 2009). Our results for the middle Paraná River agree and highlight that the most favourable conditions were recorded when floods occurred in late spring or summer

(SSF), had an intensity > 6 m and duration > 80 days (Figures 4, 6). These frequent SSF events seem to produce better scenarios in the floodplain for commercial fisheries, enhancing spawning success and survival of juveniles (Bailly *et al*., 2008). This generally results in abundant catches for two years after the optimal event (Quirós and Cuch, 1989; Rabuffetti *et al*., 2016). The aforementioned is clearly exemplified by the increase in commercial catches of *P. lineatus* in the period between 1962 and 1964 in the floodplain, after the occurrence of the great SSF of 1959 ($H_{\max}$ 6.12 m, 160 flooded days). Moreover, larger sizes were predominant in 2013–2015 after the SSF of 2009–2010 (Figures 5, 6), showing that the lag required for the species seems to be 4 years. This would be the time necessary for the legally exploited biomass (*e.g*., for legally allowed sizes at which they can be caught) to be dominant within the fish stock, this being the product of a successful cohort caused by such optimal conditions. Similar results were postulated by Quirós and Cuch (1989) and Espinach Ros *et al.* (2012) for the Paraná River.

It is important to note that the composition of commercial assemblages changed over time in the middle Paraná River, highlighting the loss of species of great commercial value [*e.g*., *Piaractus mesopotamicus* (Holmberg 1887), *S. brasiliensis* and *Zungaro jahu* (Ihering 1898)] since the 1980s. These species have been replaced by others of minor value (*e.g*., *H. aff. Malabaricus, Pterodoras granulosus* (Valenciennes 1821); Figure 4; Fuentes & Quirós, 1998; Quirós, 1990; Baigún *et al.*, 2013). In addition, a decrease in *P. lineatus* mean size from 48 to 42 cm has been recorded since 2000, which was probably caused by a reduction in mesh size from 16 to 12 cm (Baigún *et al.*, 2013).

Our results also show that by comparing the size structure of LM species after different SSFs. Although catches and biomass of juveniles always increase, floods do not bring about the same response in assemblages. Lower SSFs ($H_{\max} < 5.3$ m, duration < 70 days) do not have markedly beneficial effects on reproduction in the floodplain system at least for all LM commercial species (Figure 6). Moreover, after SSFs of a great duration (> 80 days) and high intensity ($H_{\max} > 6$ m) such as those in 1965–1966 and 2015–2016 (Supporting Information Table S1), the size range of juveniles was markedly smaller than after the SSF of 2010 (Figures 5, 7), which produced the most successful cohort of the decade. In comparison with this, SSFs showed rapidly rising slopes (Date$H_{\max}$ 9 February 2010 *v*. 5 January 2016, markedly more pronounced) and in both delay was higher (18 November 2009 *v*. 29 December 1965 and 12 December 2015, flood starting almost in summer).

In this sense, the difference observed in recruitment can be explained by the abrupt rise of SSF, which might negatively affect reproduction, development of pre-spawning processes and spawning and breeding season, egg production and larvae washing out into floodplains (Junk *et al*., 1989; Welcomme & Halls, 2004). Another factor to be considered may be delay: floods starting in late summer in most river–floodplain systems could lead fish to fail to spawn or result in poor growth and low survival of young fish (Welcomme & Halls, 2004). Gonadal maturation of LM species is stimulated by increasing temperature, while the beginning of spawning has been more related to the beginning of floods (Suzuki *et al.,* 2004, 2009; Vazzoler, 1996). These factors are responsible for reproductive success. The optimum conditions for recruitment on floodplains should occur when rises in temperature and flows coincide (King *et al.*, 2003), in addition to high intensity and duration of SSFs, these being the most favourable hydrological conditions for fisheries conservation.

On the other hand, the low recruitment and large-size of LM reported during periods of AF or WF (*e.g.*, 2011, 2013–2015; Figure 6), outside the period of greatest probability of spawning (Abrial *et al.*, 2018; Agostinho *et al.* 2004; Oliveira *et al*., 2014), indicate negative effects of floods on reproduction and recruitment of the commercial assemblage. In addition, the abrupt decrease in catches of *P. lineatus* since 1944, especially from May 1944 to mid-1945, was correlated with the beginning of the longest and most intense disconnection event of the past 130 years, which would have produced unfavourable conditions for fish reproduction, recruitment and survival (Gómez, 2015; Gonzales Naya *et al*., 2011; Figure 8). Floods out of phase with the highest temperatures (such as AF, WF) and a warm period marked by low connectivity lead to the worst conditions for recruitment of most species (Abrial *et al*., 2018), especially for LM. These results highlight the crucial role of hydroclimatic conditions recorded over humid-dry periods to explain minimum and maximum commercial catches of LM species, which shows a strong synchronism between optimum hydrological events (*e.g*., SSF 2009–2010) and recruitment.

This work shows that SSFs of > 80 days, > 6 m, $H_{\max}$ and in which rises in temperature and flows coincide (delay), and rise slopes are not pronounced but with flood frequencies similar to those recorded during humid periods, seem to provide the optimum and necessary hydrological conditions in floodplain systems for successful recruitment of LM commercial fishes and their conservation in the middle Paraná River. The best hydrological conditions for reproductive success of inland fisheries are summarised in Table 2.

4.3 | Potential anthropogenic impacts

In addition to hydroclimatic factors, some other aspects may have influenced annual and interannual fluctuations and conditions of commercial species over time. Along the Paraná River, numerous dams have been built in the upper reaches since the 1960s (Agostinho *et al*., 2007, 2008). Dams block fish migration routes (Agostinho *et al*., 2008), producing a functional simplification in the system (Oliveira e*t al*., *2*018). In the Paraná |Basin, however, these are located *c.* 740 km upstream from the middle reaches, an unregulated free-flowing corridor of more than 1500 km that coincides with documented fish migration routes (Baigún *et al*., 2003; Bonetto & Pignalberi, 1964). The main effects produced by dams in the Paraná Basin are the increase in minimum water levels since the 1970s (Quiros, 1990), a factor that could have modified fish dynamics (Abrial *et al*., 2018).

In addition, not only the hydrological regime governs the functioning of fisheries in floodplain systems. Water quality variables, including water temperature, dissolved oxygen, ammonia, nitrates and nitrites can play a crucial role in fish recruitment and survival with positive or negative effects on fish assemblages (Zhao *et al.*, 2015). Unfortunately, this information on exact water quality at different points over time is unavailable. The hydrochemistry of the main channel but secondary and minor floodplain courses in the middle reach is adequate for both fish life and aquatic biota, according to international standards for water quality (Hammerly, 2011).

On the other hand, as regards commercial datasets, commercial fisheries of the lower La Plata Basin date back from the 1930s (Prol, 2008). From 1934 to 1943, the increase in captured volumes was constant, the most abundant catches being recorded between 1941 and 1943, after the humid period at the beginning of the 20th Century. Official statistics documented that collection and systematisation of fishery data were improved in the 1940s (Fuentes & Quirós, 1988). Despite this, catches of *P. lineatus* decreased markedly in 1944 (Figure 5), which is associated with unfavourable hydrological conditions. Sverlij and Espinach Ros (1986) postulated that it is not possible to associate direct anthropogenic factors related to fishing pressure with variation in catches, given that no significant changes in effort and number of fishers were reported from 1930 to the 1980s (Iwaszkiw & Lacoste, 2011). The hydroclimatic component gained higher significance in this period than the anthropogenic component, as quantitatively demonstrated by Rabuffetti (2018).

For the lower Paraná Basin, Baigún *et al.* (2013) identified an increase in exploitation by the end of the 20th Century. A period of intensive exploitation of fisheries was recorded between 2003 and 2006 (an overfishing period defined by Baigún *et al*., 2008, 2013; Prol, 2008; Figure 8), which is coincident with a dry climatic scenario. At that time, overfishing was not considered a factor capable of significantly distorting the statements of this study, considering that the last case was recorded under unfavourable conditions for fisheries. However, it is necessary to be alert to past-present hydroclimatic conditions in order to ensure sustainability of freshwater fisheries.

Finally, this work shows that this natural regime of the middle Paraná River is one of the outstanding ecological requirements for inland fisheries' conservation. This natural flow regime must be retained in order to sustain diversity of ecosystems and productive fisheries in this mega river. Other factors, such as overfishing and fishing effort, should be further investigated. Still, there is a consensus that the middle Paraná River remains heterogeneous and unregulated without major anthropogenic changes to the floodplain. On the other hand, with this study we identified the need to continue this research considering other possible effect, such as anthropogenic effects related to fishing activity and changes to the floodplain over time, which might affect catches in some way and structuring of commercial fish assemblages.

ACKNOWLEDGEMENTS

The authors thank Ministerio de Producción of Santa Fe Province, Subdirección General de Ecología, for allowing them to access data on fiscal fish catches (PPSF, 2011–2015). Logistic support provided by Instituto Nacional de Limnología (INALI, Argentina) is greatly appreciated.

CONTRIBUTIONS

A.P.R., L.A.E. and M.L.A. developed the research idea and defined the analysis; A.P.R., L.A.E., E.A., M.F.E and E.G.E. collected data on site; A.P.R. and L.A.E. analyzed the data; M.L.A., M.C.M.B. and L.A.E. supervised and funding the study; A.P.R. generated data and wrote the manuscript with significant contributions from all coauthors.

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SUPPORTING INFORMATION

Supporting information can be found in the online version of this paper.

TABLE 1 Commercial fish species recorded and organisations that hold the corresponding dataset

Species	**Code**	**CN**	**RS**	**PPARG**	**INALI**	**PPSF**	**LH**
Hoplias aff. *malabaricus*	*H.mal*	Tararira	PC		X	X	X
Luciopimelodus pati	*L.pat*	Patí	LM	X	X	X	
Megaleporinus obtusidens	*M.obt*	Boga	LM	X	X	X	X
Pimelodus maculatus	*P.mac*	Bagre	LM	X	X	X	X
Prochilodus lineatus	*P.lin*	Sábalo	LM	X	X	X	X
Pseudoplatystoma sp.	*Pse.*sp	Surubí	LM	X		X	
Pterodoras granulosus	*P.gra*	Armado	LM		X	X	
Salminus brasiliensis	*S.bra*	Dorado	LM	X	X		X

Code, codes used in graphs; CN, common name in Spanish; RS, reproductive strategy (PC, sedentary fish with parental care and external fertilization; LM, long-distance migratory fish with external fertilisation and without parental care); PPARG, Argentinian Continental Fishery Production; PPSF, Fiscal fishing of Santa Fe State; INALI, Argentine National Institute of Limnology, LH, Laboratory of Hydroecology.

TABLE 2 The best hydrological conditions for reproductive success of inland fisheries

	Timing	$\boldsymbol{H}_{\mathbf{max}}$	**Duration**	**Frequency**
Upper Paraná River	Spring–summer floods	>6.1 m	> 75 days	
Middle Paraná River	Spring–summer floods	>6 m	> 80 days	2–3 per decade

H_{max}, Maximum height of the flood

Legend of figures

FIGURE 1 Area of study in the middle Paraná River, Argentina. Numbers (Cod) indicate ports where data of commercial fisheries were obtained: Producción Pesquera Argentina (the Argentine inland fishery production; PPARG) 1–2; 7–8; 10 and Ministerio de Producción (Ministry of Production), Subdirección General de Ecología de Santa Fe, Sub-directorate General of Ecology of Santa Fe Province (PPSF 3–6; 9). LH: Laboratory of Hydroecology. INALI: Argentine National Institute of Limnology. *fd:* flow direction. (Modified from Rabuffetti *et al.*, 2016).

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FIGURE 2 Cluster analysis of flow regime in the study period (1920–2016) using 18 hydroclimatic variables; spring summer flood (SSF) events are highlighted in red.

FIGURE 3 (a) Maximum water levels (H_{max}) and duration of floods when water level was > 4.5 m at Sante Fe Port guage between 1905 and 2016. (b) Correlation between H_{max} and duration of floods considering only years with biological information of fishes. ◆, Spring summer flood (SSF) events are highlighted in red.

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1. Change a), b) to (a), (b)

2. Change x-axis to Duration of flood (days)
3. Change y-axis to read $H_{\max}$ (m)

FIGURE 4 Distance-based redundancy analysis (dbRDA) of year-to-year differences in commercial fish catches in the middle Paraná River from 1935 to 2016 explained and structured by flow regime variables: fisheries data from (a) PPARG, Producción Pesquera Argentina; (b) PPSF, Ministerio de Producción, Sub-directorate General of Ecology of Santa Fe Province; (c) INALI, Argentine National Institute of Limnology; (d) LH, Laboratory of Hydroecology.

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1. Label top LH panel (a), top RH panel (b), lower LH panel (c) and lower RH panel (d)

FIGURE 5 (a), (b) Interannual maximum water levels ($H_{\max}$) at Santa Fe Port gauge (—) and fluctuation of *Prochilodus lineatus* catches by institution datasets in the middle Paraná River 1935–2016. (c) catches per decade from PPARG and (d) INALI datasets. ■, Total catch; ■, adults and pre-adults; ■, Young-of-the-year; ◆, spring–summer flood events (> 4.5 m at Sante Fe Port gauge). PPARG, Producción Pesquera Argentina; PPSF, Ministerio de Producción, Sub-directorate General of Ecology of Santa Fe Province; INALI, Argentine National Institute of Limnology; LH, Laboratory of Hydroecology.

FIGURE 6 Interannual fish abundance and size structure of landed and measured fishes (total and per species) for distinct hydroclimatic conditions. —, monthly mean water level ($H_{\max}$). —, mean monthly temperature; ■, total number of individuals collected (n); ■, number of individual measured (standard length *L*s).

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1. Change Hmax to $H_{\max}$.
2. Change all n to *n* (italic).

3 Change all nLs to n L_S.

4 Change all hyphens to en dashes.

FIGURE 7 Association of sizes range of landed and measured commercial fishes with the most significant hydroclimatic variables during different hydrological conditions recorded along the studied period. (a) Argentine National Institute of Limnology (INALI) 1965–1967, 1978–1979, 1984–1985, 1992–1994; (b) Laboratory of Hydroecology (LH) (2009–2011, 2013–2015).

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1 Change a and b to (a) and (b)

FIGURE 8 Schematic representation of interannual variation of maximum water levels (H_{max}; 1935–2016) showing the influence on fish catches of hydroclimatic fluctuations (humid–dry periods). Note higher fish catches after largest spring–summer flood (SSF; ★) events ($H_{max} > 4.5$ m at Sate Fe Port gauge). Probability of anthropic influence was indicated with lines of distinct thickness. WL: water level.

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1 Change y-axis to read H_{max} (m)

2 Change Larger SpringSummer-Flood to SSF

3 Change hyphens to en dshes (no spaces)

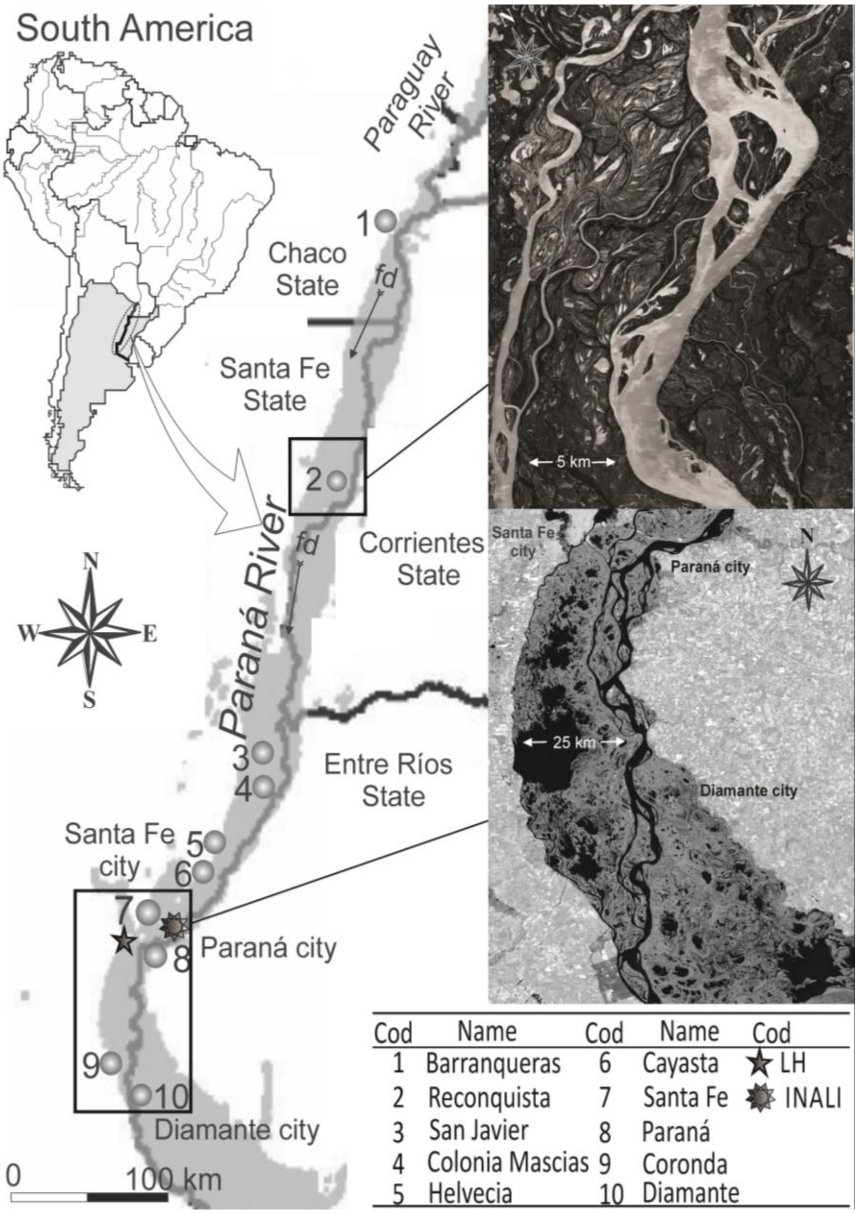
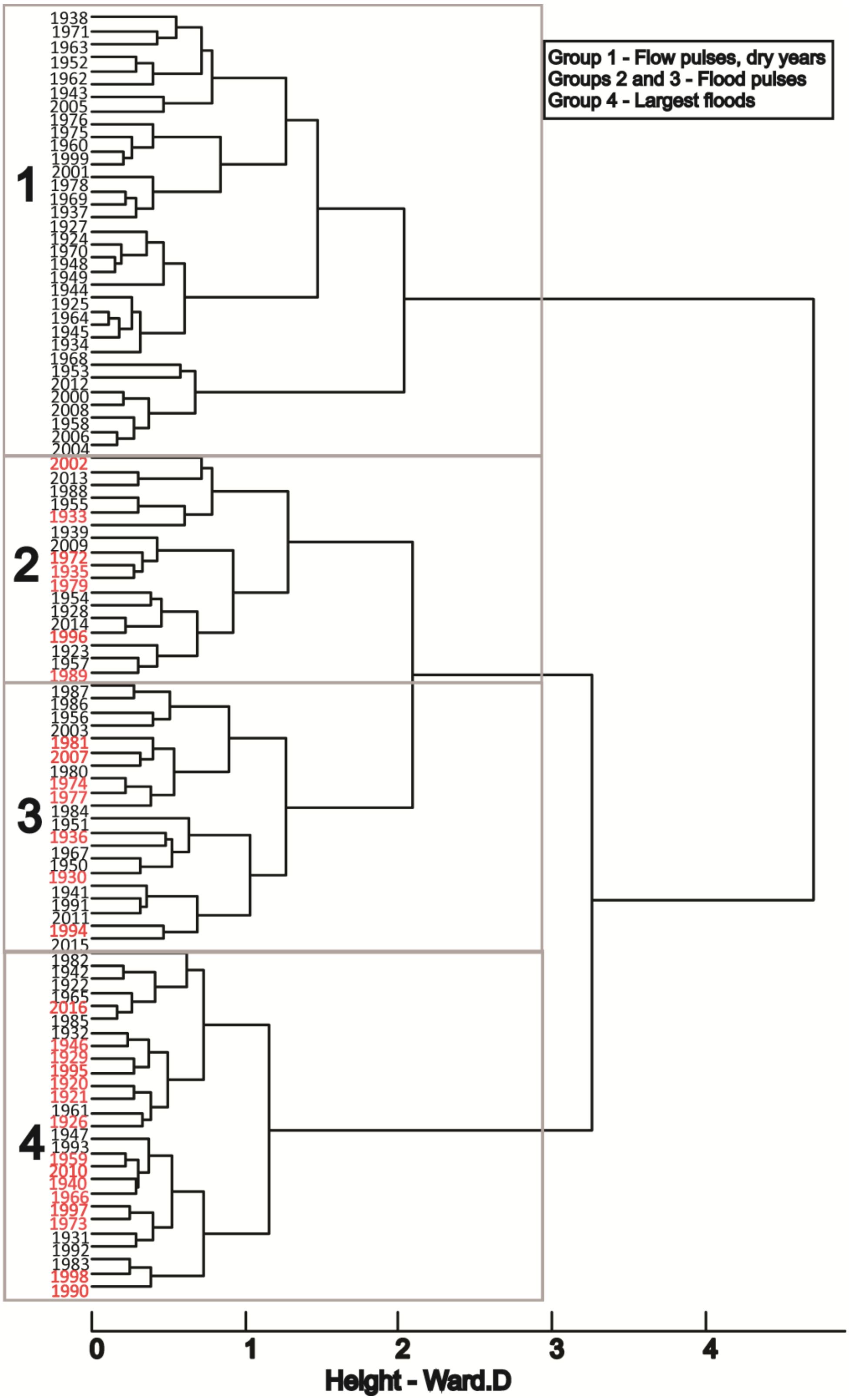

South America
Paraguay River
1
Chaco State
fd
Santa Fe State
2
Paraná River
fd
Corrientes State
N
W
E
S
3
4
Entre Ríos State
Santa Fe city
5
6
7
8
Paraná city
9
10
Diamante city
0
100 km
5 km
Santa Fe city
Paraná city
25 km
Diamante city
Cod Name Cod Name Cod
1 Barranqueras 6 Cayasta ★ LH
2 Reconquista 7 Santa Fe ✹ INALI
3 San Javier 8 Paraná
4 Colonia Mascias 9 Coronda
5 Helvecia 10 Diamante

Figure 1.


1938
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1949
1944
1925
1964
1945
1934
1968
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1966
1997
1973
1931
1992
1983
1998
1990
1
2
3
4
Group 1 - Flow pulses, dry years
Groups 2 and 3 - Flood pulses
Group 4 - Largest floods
0
1
2
3
4
Height - Ward.D

Figure 2.

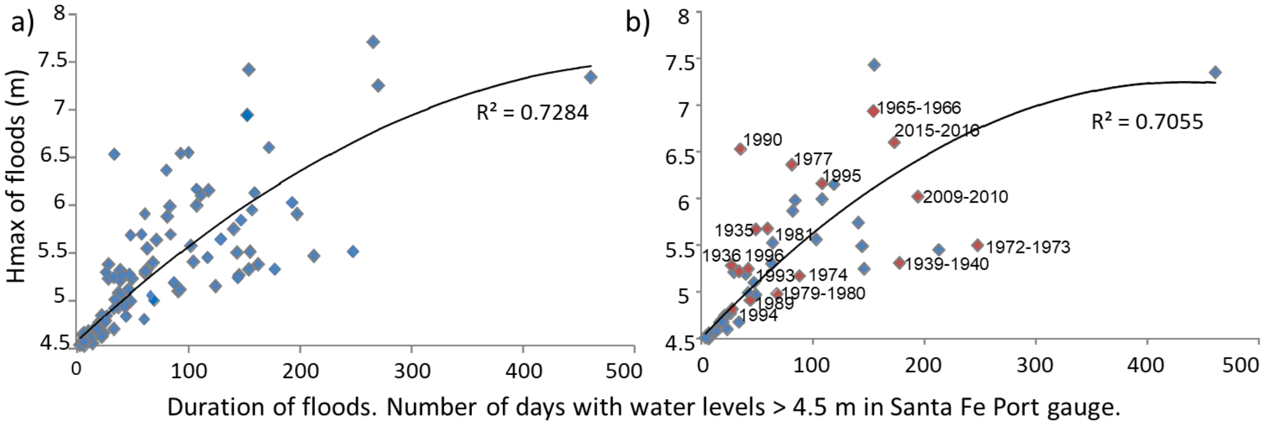


Figure 3.

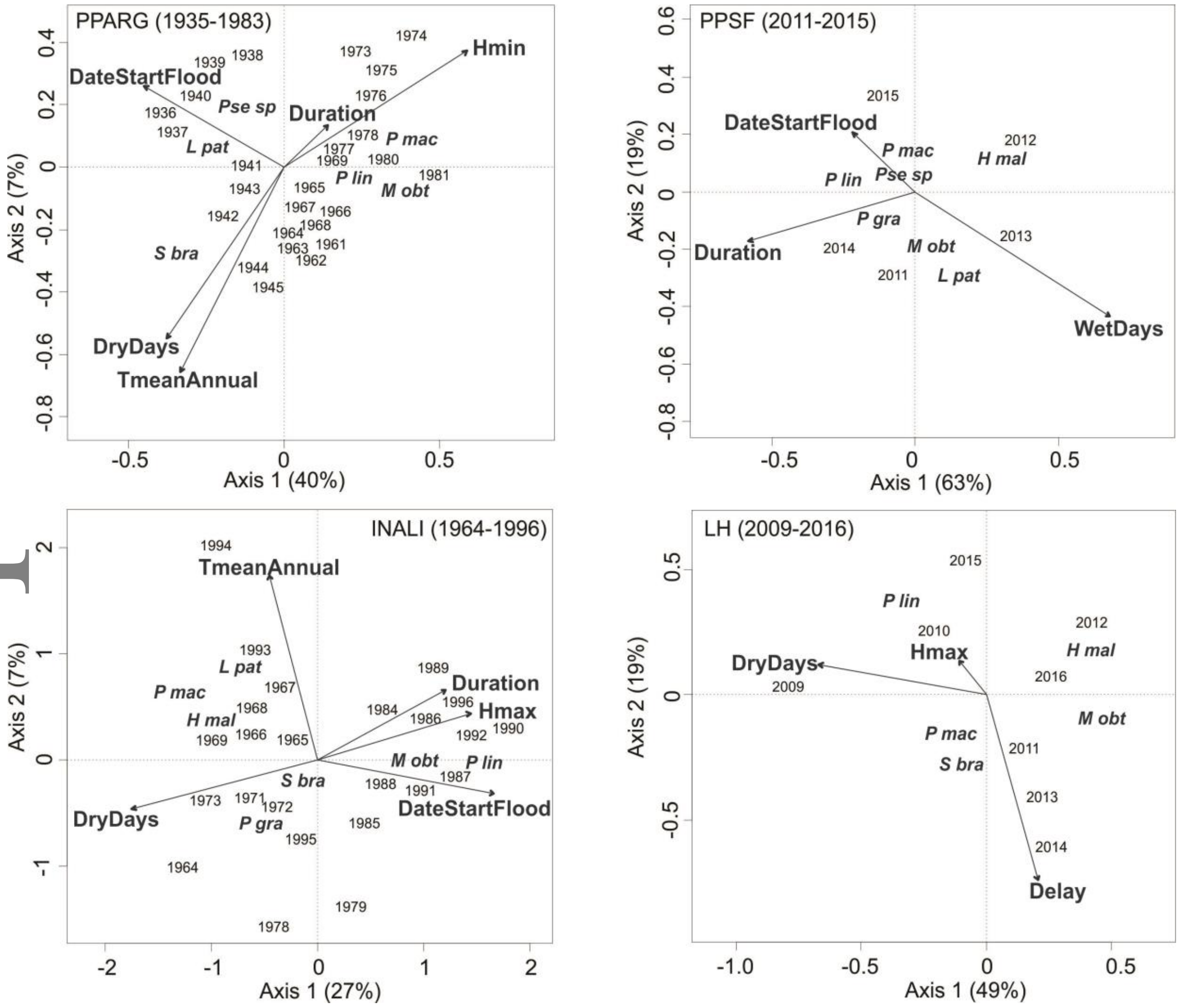
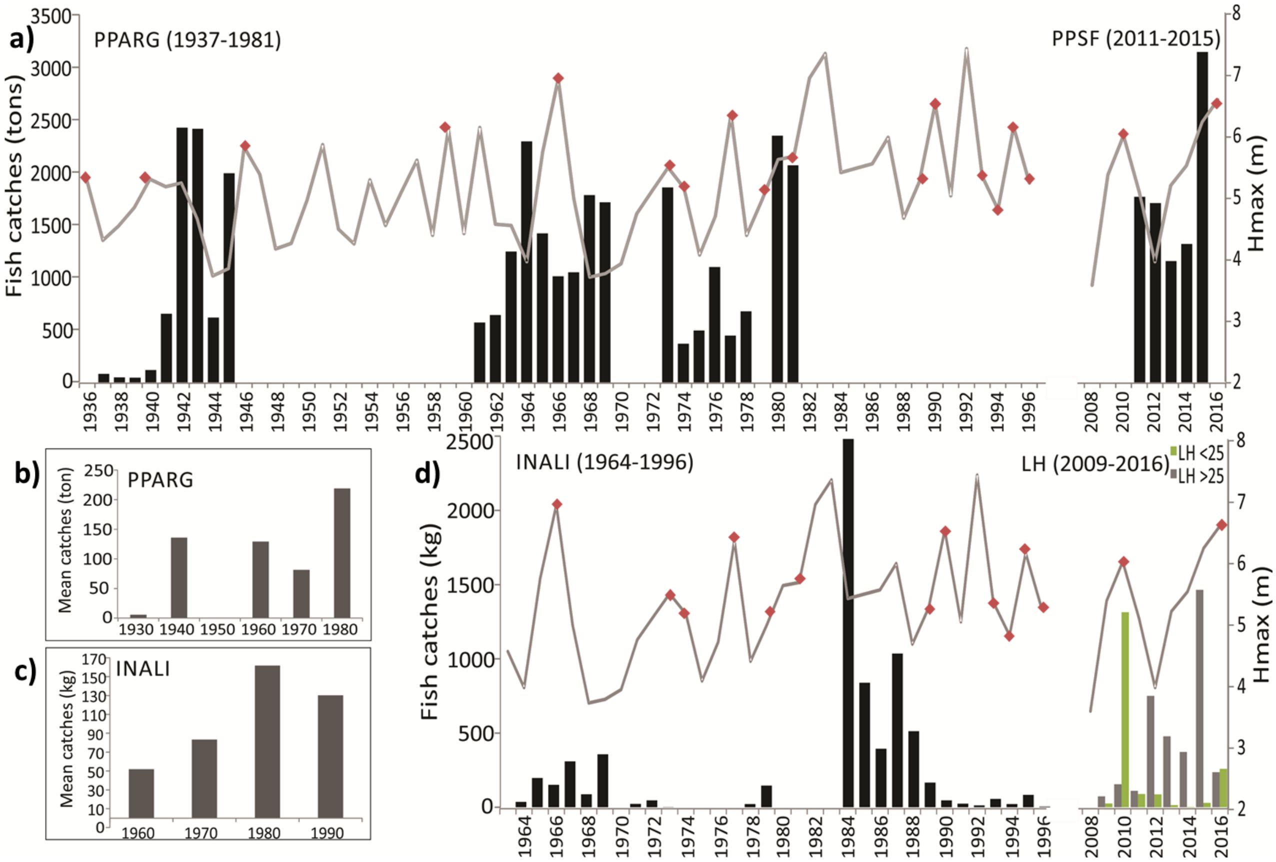


Figure 4.


a)
PPARG (1937-1981)
PPSF (2011-2015)
Fish catches (tons)
Hmax (m)
0
500
1000
1500
2000
2500
3000
3500
2
3
4
5
6
7
8
1936
1938
1940
1942
1944
1946
1948
1950
1952
1954
1956
1958
1960
1962
1964
1966
1968
1970
1972
1974
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
2008
2010
2012
2014
2016
b)
PPARG
Mean catches (ton)
0
50
100
150
200
250
1930
1940
1950
1960
1970
1980
c)
INALI
Mean catches (kg)
0
10
30
50
70
90
110
130
150
170
1960
1970
1980
1990
d)
INALI (1964-1996)
LH (2009-2016)
LH <25
LH >25
Fish catches (kg)
Hmax (m)
0
500
1000
1500
2000
2500
2
3
4
5
6
7
8
1964
1966
1968
1970
1972
1974
1976
1978
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1982
1984
1986
1988
1990
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1994
1996
2008
2010
2012
2014
2016

Figure 5.

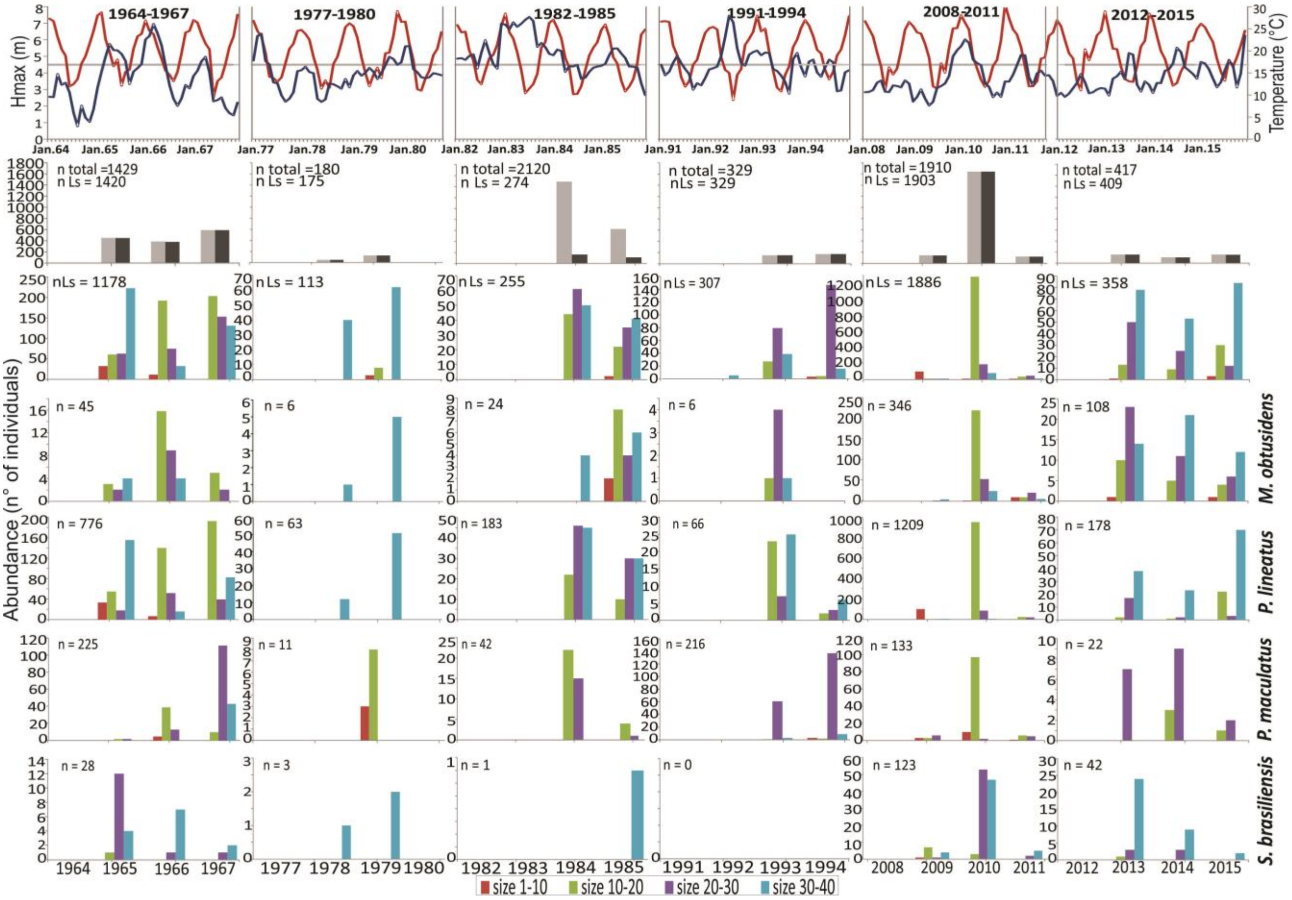

Figure 6.

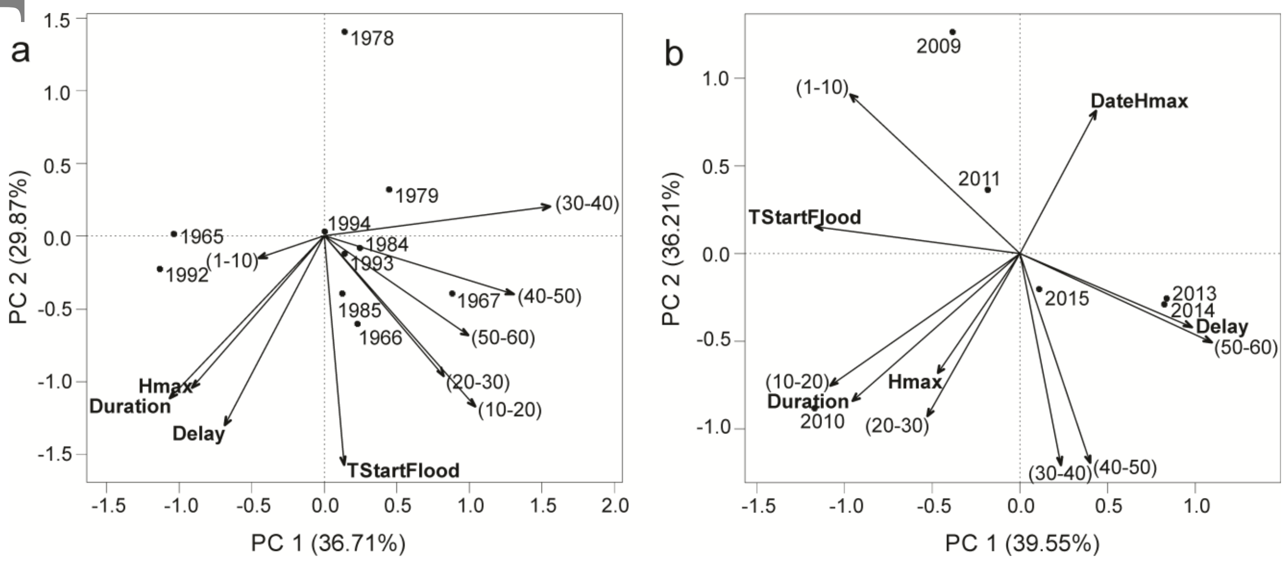

Figure 7.

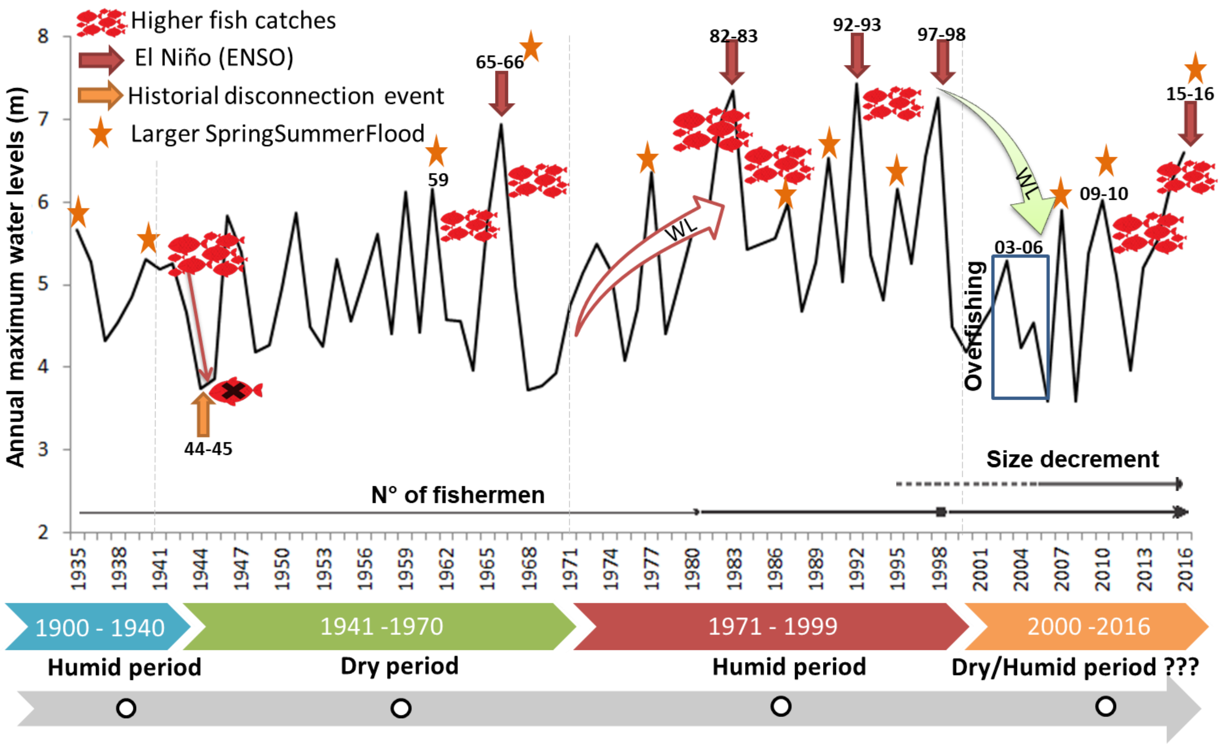
Higher fish catches
El Niño (ENSO)
Historial disconnection event
Larger SpringSummerFlood
Annual maximum water levels (m)
8
7
6
5
4
3
2
44-45
59
65-66
82-83
92-93
97-98
03-06
09-10
15-16
WL
WL
Overfishing
Size decrement
N° of fishermen
1935
1938
1941
1944
1947
1950
1953
1956
1959
1962
1965
1968
1971
1974
1977
1980
1983
1986
1989
1992
1995
1998
2001
2004
2007
2010
2013
2016
1900 - 1940
1941 -1970
1971 - 1999
2000 -2016
Humid period
Dry period
Humid period
Dry/Humid period ???

Figure 8.