



Long-term trends of fishery landings and target fish populations in the lower La Plata basin

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The La Plata basin is the second largest basin of South America and has supported important river fisheries for more than a century. In this paper, we evaluate for the first time the historical trends of landings of 21 fish taxa and the recent population trends of 27 species of commercial fishes in the lower La Plata basin (Argentina). We compiled three kinds of data sets: Total fishery landings (between 1934 and 1986) and exports (1994–2019), fisheries monitoring programs of Chaco and Santa Fe provinces in the Paraná River (2009–2019), and surveys of fish populations in the Upper (Corrientes, 1993–2020) and Middle (EBIPES, 2005–2020) Paraná River. The analysis of the historical landings showed more species declining in the lower portion of the basin than in the upper basin. Regarding recent population trends, *Pimelodus* spp., *Hoplias* spp., *Salminus brasiliensis*, *Luciopimelodus pati*, and *Ageneiosus* spp. declined in more than one region, while *Megaleporinus* spp., *Pterodoras granulosus*, and *Oxydoras kneri* showed stable to positive trends, with the other species varying in their trends between regions. These tendencies could be associated to a combination of factors such as overfishing and environmental changes that would require an ecosystem approach for their adequate management.

Keywords: Floodplains, Hydroelectric dams, Inland fish, Overfishing, Paraná River.

Submitted January 13, 2021

Accepted July 8, 2021

by Franco Teixeira de Mello

Epub Ago 25, 2021

Online version ISSN 1982-0224

Print version ISSN 1679-6225

Neotrop. Ichthyol.

vol. 19, no. 3, Maringá 2021

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La Cuenca del Plata es la segunda más grande de Sudamérica y ha soportado importantes pesquerías fluviales desde hace más de un siglo. En este trabajo, evaluamos por primera vez las tendencias históricas en los desembarques pesqueros de 21 taxones de peces y las tendencias poblacionales recientes de 27 especies de peces comerciales de la baja Cuenca del Plata (Argentina). Compilamos tres tipos de datos: desembarques pesqueros totales (1934–1986) y exportaciones (1994–2019), programas de monitoreo de pesca comercial de las provincias de Chaco y Santa Fe en el río Paraná (2009–2019), y relevamientos de peces en el río Paraná Alto (Corrientes, 1993–2020) y Medio (EBIPES, 2005–2020). El análisis de los desembarques históricos mostró más disminuciones en la porción baja de la cuenca que en la porción alta. En cuanto a las tendencias poblacionales recientes, *Pimelodus* spp., *Hoplias* spp., *Salminus brasiliensis*, *Luciopimelodus pati* y *Ageneiosus* spp., declinaron en más de un sector, mientras que *Megaleporinus* spp., *Pterodoras granulosus* y *Oxydoras kneri* mostraron tendencias estables a positivas, con las otras especies variando en sus tendencias entre regiones. Estas tendencias podrían asociarse a una combinación de factores como la sobrepesca y los cambios ambientales que requerirían una aproximación ecosistémica para su adecuado manejo.

Palabras clave: Llanuras aluviales, Peces continentales, Represas hidroeléctricas, Río Paraná, Sobrepesca.

INTRODUCTION

A growing human population and the intensification of land and water uses are threatening freshwater biodiversity and the ecosystem services it offers to local communities, such as fishing resources (Dudgeon, 2020). Inland capture fisheries provide livelihood and food security for millions of people around the world, being a valuable source of protein-rich food and employment, and offering enormous recreational and economic benefits (Funge-Smith, Bennett, 2015). Inland fisheries face a great number of threats by overfishing; alternative uses of water for hydropower generation, irrigation and human consumption; pollution and run-off from agriculture; industrial and urban activities; and climate change (Allan *et al.*, 2005; Youn *et al.*, 2014; Winemiller *et al.*, 2016; Harrod *et al.*, 2018). Fisheries of tropical and subtropical large river basins are complex systems, because they operate over ecologically diverse assemblages using multiple gears, exhibit high interannual variability strongly affected by environmental variables, and develop under ever changing social and economic contexts. In addition, the monitoring of landings is difficult because of the diffuse and small-scale nature of individual fisheries, the location of landing sites in remote and inaccessible rural areas, and because much of the catch goes directly to domestic consumption (Welcomme *et al.*, 2010). The steady grow of 3% by year of freshwater fish landings in the last decades (FAO, 2020), seems to mask the decline of several high-valued large-bodied migratory species affected by habitat fragmentation and overexploitation, and the replacement by low-valued small non-migrant species (Allan *et al.*, 2005). For this reason, the evaluation

of the trends in the landings of individual species and the state of wild fish populations over large temporal scales is critical to evaluate both the sustainability of fisheries and the healthy functioning of ecosystems.

South America is the continent with the highest concentration of surface freshwater, and contains several of the largest rivers in the world (Latrubesse, 2008), with huge and highly productive floodplains that host the greatest biodiversity of fish on the planet (Reis *et al.*, 2016; Albert *et al.*, 2020). In these environments, multispecific fisheries have developed focused on large migratory fish, such as piscivorous pimelodid catfishes (*Brachyplatystoma* Bleeker, 1862, *Pseudoplatystoma* Bleeker, 1862, *Zungaro* Bleeker, 1858), detritivorous prochilodontids (*Prochilodus* Agassiz, 1829, *Semaprochilodus* Fowler, 1941), and herbivorous serrasalמידs (*Colossoma* Eigenmann & Kennedy, 1903, *Piaractus* Eigenmann, 1903) (Barletta *et al.*, 2010; Barletta *et al.*, 2016). Although South American fisheries are among the least exploited on the planet (Welcomme, 2010), several fisheries suffered the decline of their main species and even others totally collapsed (Agostinho *et al.*, 2007; Castello *et al.*, 2015; Barletta *et al.*, 2016). As in other parts of the world, South American fisheries have received little government support for monitoring and management, which has led to their undervaluation as a source of livelihood, poor quality or absence of fishery statistics, and wrong management decisions that resulted in environmental, social and economic problems (Agostinho *et al.*, 2007b; Barletta *et al.*, 2016). Except for the clearly documented declines of migratory species associated with the installation of dams (Sato, Godinho, 2003; Agostinho *et al.*, 2007; Hoeninghaus *et al.*, 2009; Van Damme *et al.*, 2019), declines have rarely been associated to particular causes but rather to a synergy of factors, among which overfishing, pollution, environmental fragmentation and changes in land use at the basin level operate in combination (Barletta *et al.*, 2016; Castello *et al.*, 2018). In the different rivers of the continent, declines have been repeatedly observed in the same genera of large-bodied species such as *Arapaima* Müller, 1843, *Brachyplatystoma*, *Pseudoplatystoma*, *Zungaro*, *Colossoma*, *Piaractus*, and *Prochilodus*, among others.

The La Plata basin is the third largest basin in the world and comprises the Paraná, Paraguay, and Uruguay rivers. The east upper region of the basin (the Upper Paraná), located in Brazil, has been severely regulated and fragmented by dams, whereas the west portion conforms a large unregulated sub-basin from the upper Paraguay River to the Río de la Plata estuary, that still exhibits large floodplains and free-flowing river channels. The more than 770 dams installed in the Upper Paraná River basin (SNIRH, 2021) and the intense deforestation caused changes in the natural hydrological and nutrient regime (Bonetto *et al.*, 1989; Quirós, 2004; Amsler *et al.*, 2007; Lee *et al.*, 2018), whereas the growth of urban, industrial, agricultural and mining activities generated pollution with sewage discharges, heavy metals and agrochemicals (Ronco *et al.*, 2016; Avigliano *et al.*, 2019; Nogueira *et al.*, 2021). The original fisheries targeted large migratory species, such as the predatory *Salminus brasiliensis* (Cuvier, 1816), *Pseudoplatystoma* spp., and *Zungaro jahu* (Ihering, 1898) and the fruit-and-seed eater *Piaractus mesopotamicus* (Holmberg, 1887) (Petrere Jr *et al.*, 2002; Quirós *et al.*, 2007; Hoeninghaus *et al.*, 2009), with an increasing importance of the detritivorous *Prochilodus lineatus* (Valenciennes, 1837) in the lower reaches (Quirós, 1990; Espinach Ros, Fuentes, 2000; Quirós *et al.*, 2007). Although total landings and estimation of mortality rates of some species suggest a low exploitation level of the fishery of the lower La Plata basin (Quirós, Cuch, 1989;

Espinach Ros *et al.*, 2012), in the last decades several species showed population declines and even disappearance in the landings (Quirós, 1990; Lucifora *et al.*, 2017).

Fishery statistics for the Argentine sector of the La Plata basin began as early as 1921, but they were discriminated by landing site and species only after 1934 (Fuentes, Quirós, 1988; Rabuffetti *et al.*, 2017). The collection of statistics continued until 1987 when it was interrupted, and since 1994 only total exports by species are reported (Iwaszkiw, Lacoste, 2011). These data have been partially used in several studies to analyze the spatial and temporal changes in the composition of the landings (Fuentes, Quirós, 1988; Quirós, Cuch, 1989), the relationship between the change in the hydrological regime and the anthropic factors on the landings (Quirós, 1990; Rabuffetti *et al.*, 2017; Rabuffetti *et al.*, 2020), and the temporal trends of exports in the last decades (Iwaszkiw, Lacoste, 2011). However, at present there are no detailed analysis of long-term trends in the landings of individual species and population trends for most species are completely unknown. In the last decades, several monitoring programs have been collecting detailed information on fishery landings and fish abundance of wild populations (Espinach Ros *et al.*, 2012; del Barco *et al.*, 2016; Vargas, 2020), which provide a good opportunity to analyze landing and fish population trends of the main species. The only group of species in which population trends have been studied are the stingrays of the genus *Potamotrygon* Garman, 1877, some of which appear to be declining in association with higher fishing pressure in the Middle and Lower Paraná River (Lucifora *et al.*, 2017). Our approach here is to compile all the information available on fishery landings and fish abundance of the lower (southern) La Plata basin to describe the trends in landings from 1934 to the present and analyze the current population trends of the main species of the fishery.

MATERIAL AND METHODS

Databases (general description and history). We analyzed six different databases, which together covered the period between 1934 and 2020: 1) historical official statistics of fishery production of Argentina, including total landings by species from La Plata basin (1934–1986) and 2) total fish exports by species (1993–2019); 3) commercial fishery monitoring of Santa Fe (2009–2019), and 4) Chaco provinces (2010–2019); and two long term surveys of fish populations from 5) Corrientes Province (1993–2020) and 6) EBIPES project (2005–2020).

Fishery production of Argentina. Continental fishery statistics of Argentina were obtained from annual reports published by Argentina's National Fisheries Authority between 1920 and 1987. Landing data were reported in total weight in kg or metric tons, by species, and were detailed in a monthly or annual basis for a number of landing sites that varied among years (totalizing 113 landing sites) distributed along the Uruguay, La Plata, Paraná, Paraguay, and Bermejo rivers. Landings by species were available only between 1934 and 1986 and from 83 sites distributed throughout the lower La Plata basin (Fig. 1). Twenty fish taxa were included, but the number of species is surely higher because the records mentioned species by common names, and each name can include several species or genera (Tab. 1). Estuarine species of the genera *Pogonias* Lacepède, 1801, *Micropogonias* Bonaparte, 1831, and *Mugil* Linnaeus, 1758, which were recorded

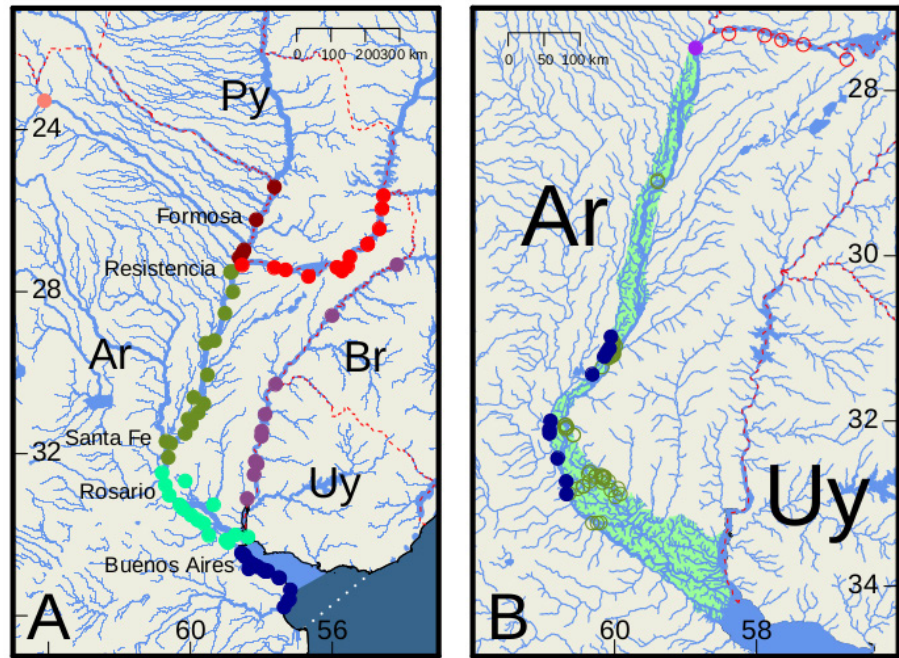


FIGURE 1 | **A.** Map of the southern region of La Plata basin showing the location of landing sites where information was collected for historical statistics of the fishery production of Argentina between 1934 and 1986. The landing sites of each river are indicated by colors; Violet: Uruguay River; Blue: Río de la Plata; Light green: Lower Paraná River; Dark green: Middle Paraná River; Red: Higher Paraná; Maroon: Paraguay; Pink: Bermejo River. **B.** Map of the southern section of Paraná River, showing landing sites and sampling localities of commercial fishery monitoring programs and surveys of fish populations, respectively. Filled blue circles indicate landing sites of commercial fishery monitoring of Santa Fe; the violet filled circle indicate the landing site of commercial fishery monitoring of Chaco; green empty circles indicate sampling sites of EBIPES survey of fish populations, and red empty circles indicate sampling sites of Corrientes survey of fish populations. The middle Paraná River floodplain and delta is shaded in bright green. Ar: Argentina; Br: Brazil; Py: Paraguay; Uy: Uruguay.

within the freshwater fishery of the Río de la Plata, were excluded from the analyses, because they are only occasionally present in freshwater areas and most fishing effort on them is applied in their marine habitat (Jaureguizar *et al.*, 2016). In this database, there was no information on fishing effort and the fishing gears used by fishermen. The lack of data about fishing effort made impossible to determine if the trends observed in the landings of each species is affected by variations in market demands and fishing activity or by fluctuations in the abundance of wild fish populations (Fuentes, Quirós, 1988). Each of these processes (*e.g.*, market demand or population fluctuations) can have a differential impact between species in different regions throughout the basin. Therefore, the landing data of Argentine fishery production should be taken with caution and interpreted as a rough estimate of the catches rather than fluctuations in the abundance or biomass of each species stocks. However, given the territorial extension and the number of landing sites included during the period, these data represent a good general estimate of the trends in the landings of each species over time.

Fish exports of Argentina. Data on exports of the most important fish species were provided by the National Service on Animal Health (SENASA, for its Spanish initials) and by the National Institute of Statistics and Censuses (INDEC, for its Spanish initials). Data were in metric tons by species by year in all the Argentine territory, without information on fishing effort, fishing gears used or the landing sites of origin. However, all species included in the analysis occur mainly within the main rivers of the La Plata basin, and all fisheries [with the possible exception of *Odontesthes bonariensis* (Valenciennes, 1835), that can be extracted from shallow lakes of the Pampean Plain (Gómez, 1998; Mancini *et al.*, 2016)] are located within the La Plata basin. These data do not include the landings destined to the domestic market and can be considered as a remnant of the internal trade, instead of the catches *per se*. For some species such as *Prochilodus lineatus*, which is scarcely commercialized in the domestic market, exports can be a good estimator of the total catches, but for species of *Pseudoplatystoma*, *Salminus brasiliensis*, and *Megaleporinus* spp., which are highly valued and commercialized in the domestic market, exports are only a fraction of total catches. In addition, different quotas have been imposed for exports of these species including the temporal or permanent closure of exports (since 2013, exports are not allowed for *S. brasiliensis*, *Pseudoplatystoma* spp., *Z. jahu*, *Pterodoras granulosus* (Valenciennes, 1821), *Oxydoras kneri* Bleeker, 1862, *Rhinodoras dorbignyi* (Kner, 1855), and *Ageneiosus* spp.), although fishing for the domestic market has continued actively. Even though, exports are the only available estimator of river fishery production of Argentina at present.

Commercial fishery monitoring of the Chaco Province. Data were provided by the Direction of Fauna and Natural Protected Areas of the Chaco Province. This monitoring program began in February 2010 and collect information to the present on a daily basis on fish landings of a number of fishermen that work at Puerto Antequera, which is placed on the main channel of the Paraná River, between the cities of Resistencia and Corrientes. The catches were monitored during the morning of working days. After each fisherman arrived at port, the catch was identified, counted, measured and weighed, and the fishing gears used and the effort applied were registered. Fishing gears were mainly drift gillnets, and longlines, and all catches took place in the main channel of the Paraná River (Vargas *et al.*, 2004). Drift gillnets were 150–300 m in length and between 2 and 3 m height, with handwoven nylon treads of mesh sizes between 16 and 30 cm between opposite knots that were used to catch the largest species (Bechara *et al.*, 2007). There were also drift trammel nets of similar length and height with two panels: one with mesh size between 16 and 25 cm and the other with approximately 50 cm in the outer wall. During each cast, these nets were deployed from a boat perpendicularly to the current, in specific areas of the river that were cleared of snags, and were pulled downstream with the current for approximately 2 km; after that, they were hauled from the boat. Longlines consisted of a main line placed over the bottom by two leads at their ends, and marked with a buoy on the surface, with 20–30 hooks baited with whole fishes (dead or alive), fish guts, snails, grasshoppers or worms. In a variant of this gear, one end of the main line was tied to the shore and the other was secured to the bottom by an anchor. For drift nets, the fishing effort was measured as the number of net casts performed by day. For longlines, the fishing effort was the number of longlines baited each day.

Commercial fishery monitoring of the Santa Fe Province. Data were provided by the Directorate of Sustainable Management of Fishery Resources of the Santa Fe Province. This monitoring program began in April 2009 and, weekly or biweekly, collected information on fish landings and fishing effort at a series of landing sites (eleven sites in total) along the floodplain of Middle and Lower Paraná River (Fig. 1B). The monitoring was performed on specific fishermen at each place. When fishermen arrived at the landing site, they declared the number of fish of each species, the number of boats used, the length of gillnets used, and the number of days fishing, to obtain the landings. During the monitoring, part of the landings (mainly *Prochilodus lineatus*) was measured in standard length of the body. The main fishing gears used in this fishery are trammel nets (del Barco, 2016). Trammel nets were generally 50 m in length and between 2 and 3 m height, with mesh sizes between 12 and 18 cm between opposite knots in the inner panel and approximately 40 cm in the outer wall. The nets were placed in floodplain lakes or rivers with very slow current. Fishing was performed by individual fishermen with one boat or by groups of fishermen of up to 10 boats. Each individual fisherman used between 50 and more than 1000 m of gillnets (median 270 m) attaching nets one to another by their ends. Fishing effort was measured as the product between the length of net used (in m), the number of boats, and the number of days fishing.

Fish populations surveys of the Corrientes Province. These data were provided by the Institute of Ichthyology of the Northeast (Instituto de Ictiología del Nordeste-Universidad Nacional del Nordeste). This long-term standardized fish sampling program collected fish samples with a monthly frequency from August 1993, in four different locations (that varied slightly through time) along the upper reach of the Paraná River between the Yacyretá Dam and the confluence with the Paraguay River (Fig. 1B). Fish were collected using standardized gillnet batteries of mesh sizes 3, 4, 5, 6, 7, 8, 12, 14, 16, 20 cm between opposite knots. Nets with mesh sizes 3, 4, 5, 6, were 15 m in length; nets with mesh sizes 7 and 8 were 18 m in length; nets with mesh sizes 12, 14, were 25 m in length and nets with mesh sizes of 20 cm were 30 m in length. Nets were placed individually on the main channel of the Paraná River in sites with slow current, perpendicular to the river axis and separated from each other by 50 m, with one end tied to the shore and the other secured to the bottom with an anchor. Nets were left during 48 h and checked every 8 h, although smaller mesh sizes could be left during 24 h to reduce mortality when catches were very abundant. Fishing effort was measured as the product between the area (length by height) of each mesh size and the time in hours that each net remained in the water during each sampling survey.

Fish populations surveys of EBIPES project. Data were provided by the project of Biological and Fishery Assessment of the Recreational and Commercially Important Fish Species of the Paraná River (Evaluación Biológica y Pesquera de las Especies de Importancia Económica del río Paraná, EBIPES). This long-term standardized fish sampling program collected fish samples seasonally, approximately four times each year from April 2005, in a number of lakes and floodplain rivers (between 5 and 16 sites per survey) in five different regions near the cities of Reconquista, Helvecia-Cayastá, Diamante, Rosario-Victoria, and Villa Constitución (Fig. 1B). Fish were collected using standardized gillnet and trammel net batteries. Gillnet batteries consisted of twelve 25

m nets attached by the ends made of mesh sizes of 3, 4, 5, 6, 7, 8, 9, 10.5, 12, 14, 16, and 18 cm between opposite knots. Since 2013, nets with small mesh size (3, 4, 5, 6, 7, and 8 cm) were shortened to 12.5 m. Trammel net batteries were 25 m in length and had inner panels with mesh size 10.5, 12, 14, 16, and 18 cm and an outer wall of 240 mm between opposite knots. All nets were made of multifilament nylon strings, except the 9 cm one, which was made of monofilament nylon strings. Each battery was tied to the shore and deployed towards the center of the lake or river, and were separated from one another to avoid interference. Nets were set at dusk, left during the night and hauled at dawn, for a period of approximately 12 h. Fishing effort was measured as the product between the length of nets (in m) of each mesh size and the time in hours that each net remained into the water during each sampling day.

In the commercial fishery monitorings (Chaco and Santa Fe) the gears used were not completely standardized and each fisherman uses slight variants of the same fishing gear and make continuous adjustments in the techniques and gears over time in relation to the hydrometric level or the behavior of the species (Liotta, 2020; Vargas, 2020) that can exaggerate or smooth out the true fluctuations in fish abundance. In addition, the fishing gears and the fishing sites are focused on the catch of target species (*Pseudoplatystoma* spp. in Chaco and *Prochilodus lineatus* in Santa Fe) and clearly underestimate the relative abundance of the remaining species in the environment. In spite of the selectivity of the gear used in favor of target species, the catch of all commercial species is landed and monitored at each site, making this data useful to evaluate the trends in CPUE even for non-target species. On the other hand, the surveys of fish populations, like EBIPES and Corrientes, carried out standardized surveys, both in terms of the fishing gear used and the sites sampled, offer more reliable estimations of the trend in the abundance of populations of each fish species.

Statistical Analyses. Historical trends in Argentinean fishery production and exports. To analyze the trends in landings or in fish population abundance of each fish species, different statistical methods were applied depending on the nature of each database. For the fishery production and exports of Argentina, that lacked fishing effort information, we analyzed the general trends in the landings of each species separately for the period 1934–1986 (landings) and 1994–2019 (only exports) by means of linear regressions, regressing annual total landings of each fish species against year (Y). The slope and intercept of the regression function were calculated by mean of the least squares technique (Zar, 1999). Confidence intervals around the slope were constructed using the bootstrap method. For each species, we evaluated the trends in biomass for all the Argentinean portion of the La Plata basin and separately for each one of the main rivers or river reaches: Río de la Plata, Uruguay, Lower Paraná (from Diamante city to the mouth), Middle Paraná (between the confluence with the Paraguay River and Diamante city), Upper Paraná (from Puerto Iguazú to the confluence with the Paraguay River), Paraná (all reaches combined), Paraguay, and Bermejo rivers (Fig. 1A). It was impossible to distinguish between years without monitoring and years without landings. Landing data for some species were not available during all years in each data set (species by river). Then, we analyzed the trends in landings only for species with ten or more years of information (consecutive or not).

Because absolute trends in landings can be affected by the monitoring effort applied

throughout the basin (which was surely variable along the period), we also analyzed the trends in the percentage of each species with respect to total landings. The percentage of landings can better reflect the changes in the relative importance of each species along time, with independence of fluctuations in either total landings or monitoring effort. The percentage of landings of each species was calculated following Quirós, Cuch (1989), and Quirós (1990) excluding *Prochilodus lineatus* from total landings, because the catch of *P. lineatus* was strongly affected by the large industrial catches of this species that took place between 1930 and 1976. Industrial fishing was performed with specific fishing gears and techniques in the Lower Paraná, Lower Uruguay river and Río de la Plata and was not related to the landings of the remaining species.

Given that the values of slopes of regression models were dependent on the absolute landings of each species (species with larger landings have larger slopes than species with smaller landings at equal rates of change), annual landings of each species were standardized dividing their values by the standard deviation of the data set of each species (Zar, 1999). This transformation did not affect the statistical significance of the slopes and was performed only to standardize the graphical representation and facilitate the comparison of the trends among species.

Current population trends of fish species in commercial fishery monitoring and surveys of fish populations. The trends in abundance of each species were analyzed separately for each data set. For commercial fishery monitoring of Santa Fe and Chaco, data were pooled on a monthly basis, and for surveys of fish population databases, data were analyzed by sampling surveys (monthly surveys in Corrientes; and seasonal surveys in EBIPES). For each site and date, we registered: year (Y), latitude (La), longitude (Lo), hydrometric level of the nearest gauge station (HL), and the abundance of each of the 20 commercially most important species of the basin (see Tab. 1). Because each gauge station differs in the mean and the variability of HL , we calculated a standardized value of HL (HL_{st}) by subtracting the mean hydrometric level of the sampling period of each database (ranging from 10 to 27 years) from the daily HL and divided this value by the standard deviation of the HL within the same period. HL_{st} was included to control the immediate effects of hydrometric level on fish catch, because it can generate an effect of dilution on fish abundance, stimulate changes in habitat use by fish or reduce the efficiency of fishing gears. We also created a seasonality index (SI) using a sinusoidal function that varied along the year with a maximum value of 1 on December 21st (beginning of southern hemisphere summer) and a minimum of -1 on June 21st (beginning of southern hemisphere winter) which was used to simulate seasonal variation along the year. This index was included to control for the effects of seasonal migratory movements or reproduction on fish abundance. For the Chaco data set, a variable identifying the type of fishing nets or the type of hook fishing gear was included, as more than one fishing gear was used in this fishery.

To analyze the trends in abundance of each species, we build generalized linear models for each species separately for each database, using the number of individuals as dependent variables and Y , La , Lo , HL_{st} , and SI as independent variables. For Santa Fe and EBIPES databases, which have sites located along a section of the Paraná River that runs in north-south direction, we used La but not Lo . For the Corrientes database, which has sites located along a section of the Paraná River that runs in east-west direction, we

used *Lo* but not *La*. Geographic coordinates were not included in the species models of Chaco database, because it consisted of only one landing site. All models included the logarithmized fishing effort ($\log(\text{ef})$) as an offset term, an error structure with negative binomial distribution and a log link (Baum *et al.*, 2003; Ferretti *et al.*, 2008). We used the negative binomial distribution because all databases had a large number of zeroes, making the variance much larger than the mean and because numerical abundance is a discrete variable. For each model, we applied a stepwise procedure, removing successively a different independent variable from the full model (*i.e.*, the one with all independent variables), and calculating the Akaike Information Criterion (AIC) at each step. The model with the lowest (AIC) was selected as the best one that described the data (Anderson *et al.*, 2000). The coefficient of the variable *Y* in each model was used to estimate the instantaneous population growth rate (*r*) for each species. We constructed 95% confidence intervals around the estimated value of *r* for each species, based on the log-likelihood profiles of the estimated *r* (Hilborn, Mangel, 1997; Barrowman, Myers, 2003). For each model, we varied the value of *r* over a sufficiently large interval including its maximum-likelihood estimation, to build a log-likelihood profile. Then, 95% confidence intervals were computed from the log-likelihood profile, by applying cutoff values derived from a chi-square distribution on one degree of freedom (Hilborn, Mangel, 1997; Barrowman, Myers, 2003). These confidence intervals were plotted in the form of “raindrop plots”, which provide information not only on the range of the confidence interval, but on the most and least likely values of the parameter within the given interval (Barrowman, Myers, 2003). For each species, we computed Akaike weights as a measurement of support of the best model and of the effect of the variable *year* on the abundance. Akaike weights can be interpreted as the likelihood of a hypothesis to be true, given the data (Franklin *et al.*, 2001). All statistical modelling was conducted using the package MASS (Venables, Ripley, 2002), of the R statistical language, version 3.6.3 (R Core Team, 2020).

RESULTS

General description of the fishery. Annual fishery production of Argentina for the period 1934–1986 varied between 1208 (1972) and 20810 t (1942), with a median of 10927 t (Fig. S1). The most exploited species during this period was *Prochilodus lineatus* that accounted for 73.5% of the total landings (Tab. 1), followed by *Pseudoplatystoma* spp. (5.8%), *Luciopimelodus pati* (Valenciennes, 1835) (4.5%), *Salminus brasiliensis* (2.5%), and *Megaleporinus* spp. (1.6%). The fishing of *Prochilodus lineatus* for industrial purposes (to obtain fishmeal and oil) represented an average of 73.8% of total landings of *P. lineatus* between 1934 and 1956 and diminished to 53.6% for the period between 1961–1976, after which the industrial exploitation of the species stopped. Annual fish exports for the period 1994–2019 varied from 3043 (1994) and 39855 t (2004) with a median of 18386 t. The most exploited species during this period was *Prochilodus lineatus* with 85.0% of total exports of freshwater fishes (Tab. 1), followed by *Hoplias* spp. (3.9%), *Megaleporinus* spp. (3.1%), *Odontesthes bonariensis* (1.3%), and *Cyprinus carpio* Linnaeus, 1758 (1.2%).

TABLE 1 | Relative importance of fish species in each of the data bases analyzed. %W is the percentage in weight of total landings; % Ab. is the percentage of abundance (in number of individuals) of the total catch. Total weight and total abundance of each database are shown in the last row, below the columns of % W and % Ab., respectively.

Species	Common name	Fish. Prod. Arg. (1934–1986)	Fish. Export. Arg. (1994–2019)	Comm. fisheries Santa Fe	Comm. fisheries Chaco		EBIPES survey		Corrientes survey	
		% W	% W	% Ab.	% Ab.	% W	% Ab.	% W	% Ab.	% W
<i>Prochilodus lineatus</i>	Sábalo	73.54	84.95	88.06	17.62	9.51	11.63		13.70	32.73
<i>Pseudoplatystoma</i> spp.	Surubí	5.80	0.55	0.40						
<i>Pseudoplatystoma corruscans</i>	Surubí pintado				14.93	44.23	0.27		0.24	3.22
<i>Pseudoplatystoma reticulatum</i>	Surubí atigrado				2.79	5.18	0.03		0.17	2.64
<i>Megaleporinus</i> spp.	Boga	1.65	3.09	4.46	4.90	3.19	3.79		5.28	8.05
<i>Luciopimelodus pati</i>	Patí	4.48	1.19	0.27	9.93	15.86	0.22		0.05	0.24
<i>Salminus brasiliensis</i>	Dorado	2.50	0.40	0.15	5.82	7.99	1.36		2.74	7.35
<i>Hoplias</i> spp.	Tararira	0.58	3.93	5.16			3.44		0.41	0.17
<i>Odontesthes bonariensis</i>	Pejerrey	2.05	1.27				0.22		0.01	0.0004
<i>Pterodoras</i> and <i>Oxydoras</i>	Armado	1.12	0.03							
<i>Pterodoras granulatus</i>	Armado común			0.64	9.29	3.58	0.39		0.66	1.69
<i>Oxydoras kneri</i>	Armado chancho			0.12	0.43	1.19	0.43		1.26	3.16
<i>Zungaro jahu</i>	Manguruyú	0.22	0.005		2.23	4.51	0.00		0.02	0.10
<i>Piaractus mesopotamicus</i>	Pacú	0.89			1.81	0.99	0.01		0.12	0.53
<i>Ageneiosus</i> and <i>Sorubim</i>	Manduvé	0.10	$1.14 \cdot 10^{-6}$							
<i>Ageneiosus</i> spp.	Manduvé			0.45						
<i>Ageneiosus militaris</i>	Manduvé fino				0.18	0.03	1.33		0.04	0.05
<i>Ageneiosus inermis</i>	Manduvé cabezón				1.26	4.92	1.26		0.14	0.24
<i>Rhamdia</i> spp.	Bagre sapo	1.32	0.26	0.01			0.05		0.01	0.001
<i>Pimelodus maculatus</i>	Bagre amarillo	0.37	$7.62 \cdot 10^{-7}$	0.16	15.34	1.50	3.08		6.01	3.38
<i>Pimelodus albicans</i>	Moncholo	0.85	$5.72 \cdot 10^{-4}$	0.11	6.68	1.14	0.15		0.04	0.05
<i>Sorubim lima</i>	Manduvé cucharón			0.01	0.39	0.09	0.14		0.83	0.75
<i>Parapimelodus valenciennis</i>	Bagarito	0.48								
<i>Hemisorubim platyrhynchus</i>	Tres puntos				0.08	0.03			1.33	2.93
<i>Pinirampus pirinampu</i>	Patí bastardo				0.59	0.20			0.01	0.02
<i>Pseudopimelodus mangurus</i>	Manguruyú Amarillo				0.16	0.11	0.16		0.01	0.02
<i>Megalonema platinum</i>	Patí bastardo				0.91	0.07			0.05	0.01
<i>Brycon orbignyanus</i>	Salmón de río	0.05			0.00	0.00	0.30		0.14	0.22
<i>Lycengraulis grossidens</i>	Anchoíta	0.52								
<i>Plagioscion ternetzi</i>	Corvina	0.00			0.01	0.00			0.53	0.61
<i>Potamotrygon</i> spp.	Raya	0.02		0.00			0.16		0.09	0.22
<i>Cyprinus carpio</i>	Carpa		1.23	0.01			0.01			
Other species		3.45	3.09	0.00	0.28	0.06	72.33		66.11	31.60
Total (Kg or number of individuals)		586348259	524654434	97219	55084	265135	139575		135045	131043

Historical trends in Argentinean fishery production and exports. A summary of the data of the Argentinean fishery production (1934–1986) and exports (1994–2019) used in this study is shown in Tab. S1. The general trends of annual landings between 1934 and 1986 for each species in the different rivers of the Argentinean portion of the La Plata basin are shown in Fig. 2. Out of 20 assessed species, eight species (40%) showed negative trends throughout the basin, whereas six species (30%) showed positive trends, and the six remaining species did not show any significant trend. Among the most important species, *Prochilodus lineatus*, *Salminus brasiliensis*, *Odontesthes bonariensis*, and *Piaractus mesopotamicus* showed negative trends, mainly in the southern end of the basin, in the Lower Paraná and Uruguay rivers, and in the Río de la Plata. In the same period, *Pseudoplatystoma* spp., *Megaleporinus* spp., *Pterodoras granulosus*, *Oxydoras kneri*, *Ageneiosus* spp., and *Sorubim lima* (Bloch & Schneider, 1801) showed positive trends. The Lower Paraná and Uruguay rivers, and the Río de la Plata had many more species with negative trends than the Middle Paraná, Upper Paraná, Paraguay and Bermejo rivers. Trends in the percentage of landings of each species followed very similar patterns with respect to absolute landings (Fig. S2).

Reliable data on fish exports of Argentina were available only for the ten most important species and for the period between 1994 and 2019 (Fig. 3). Average annual fish exports in metric tons between 1994 and 2019 of *Hoplias* spp., *Megaleporinus* spp., and *Prochilodus lineatus* were, respectively, 11.6, 3.2, and 2.0 times higher than the average annual fishery landings between 1934 and 1986. Exports of *Prochilodus lineatus* increased from 1994 to 2004, with an historical peak of 37597 t in 2004, and decreased because of the setting of a quota until 2008, and then increased gradually until the present (see Fig.

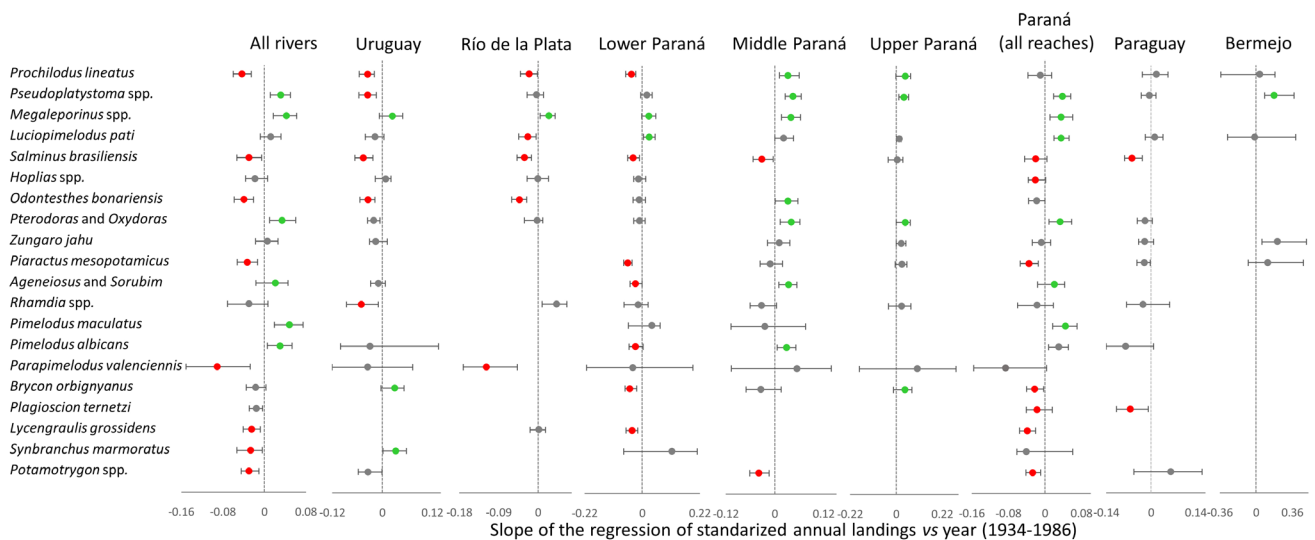


FIGURE 2 | Trends in annual landings of 20 freshwater fish taxa in the historical fishery production of Argentina (1934–1986) for all rivers of the La Plata basin and separately for each one of the rivers. Symbols represent the slopes of the linear regressions between the annual landings and year. Red symbols indicate slopes with significant negative values, green symbols indicate slopes with significant positive values and grey symbols indicate slopes not significantly different from zero. Whiskers around each symbol indicate 95% confidence intervals generated by bootstrap method.

S3 for details in the trends of landings among years). In the same period, average annual exports for *Pseudoplatystoma* spp., *S. brasiliensis*, and *L. pati* were 6.1, 3.6 and 2.2 times lower than average fishery landings between 1934 and 1936, respectively. Between 1994 and 2019, exports had negative trends for *Pseudoplatystoma* spp., *S. brasiliensis*, *Ageneiosus* spp. and *S. lima* (with exports closed since 2013), and *C. carpio*, whereas *O. bonariensis* showed a positive trend (Fig. 3). The exports of *Luciopimelodus pati*, *Hoplias* spp., and *Rhamdia* spp. did not show any significant trend. The trends in percentage of each species in exports between 1994 and 2019 can be seen in Fig. S4. The evolution of absolute and percent landings among years by species, for each river, are in Figs. S4–S8.

Recent population trends of fish species in commercial fishery monitoring and surveys of fish populations. The landings of the commercial fishery of Chaco, placed on the main channel of the Paraná River, downstream the confluence with the Paraguay River, were dominated by *Pseudoplatystoma corruscans* (Spix & Agassiz, 1829) (44.2% in weight), followed by *L. pati* (15.9%) and *Prochilodus lineatus* (9.5%; Tab. 1). The analysis of this fishery showed that 16 out of 19 species had stable or positive trends in the landings between April 2009 and December 2019, according with the

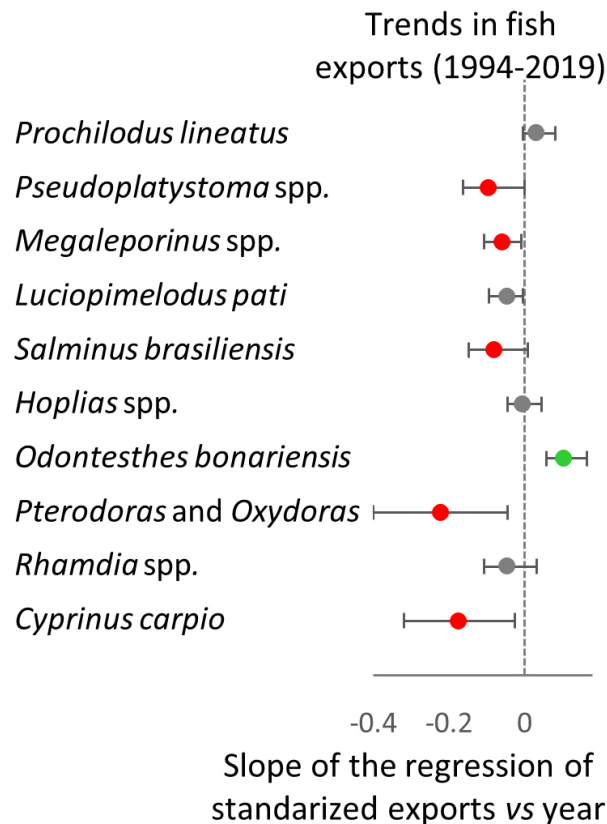


FIGURE 3 | Trends in annual freshwater fish exports of Argentina of 10 taxa between 1994 and 2019. Symbols represent the slopes of the linear regressions between the annual exports and year. Red symbols indicate slopes with significant negative values, green symbols indicate slopes with significant positive values and grey symbols indicate slopes non significantly different from zero. Whiskers around each symbol indicate 95% confidence intervals generated by the bootstrap method.

estimations of intrinsic population growth rates (Fig. 4). In general, estimations for gillnets had narrower confidence intervals than for longlines (hooks), owing to the fact that sample size was usually larger for gillnets than for longlines (Fig. 4). In comparison with drift gillnets, longline landings could be affected by a larger number of factors over time (like the availability of effective baits and changes in feeding behavior) that makes the landings more variable over time.

For most species, the trends in the landings were similar between the estimations for drift gillnets and longlines. The species *Salminus brasiliensis* and *Ageneiosus inermis* (Linnaeus, 1766) showed negative trends in the landings of drift gillnets, but showed stable trends in the longline landings. An effect of the variable Year was well supported by high Akaike weights in both gears for *L. pati* (negative), *Z. jahu* (positive), and *Pimelodus albicans* (Valenciennes, 1840) (positive) (Fig. 4; Tab. S9). The effect of Year was well supported in gillnets only for *Megaleporinus* spp. (positive), *S. brasiliensis* (negative), *P. granulatus* (positive), *P. mesopotamicus* (positive), *A. inermis* (negative), and *Pseudopimelodus mangurus* (Valenciennes, 1835) (positive) (Fig. 4; Tab. S9). The effect of Year was well supported only in longlines for *Pimelodus maculatus* Lacepède, 1803 and *Pinirampus pirinampu* (Spix & Agassiz, 1829) (Fig. 4; Tab. S9).

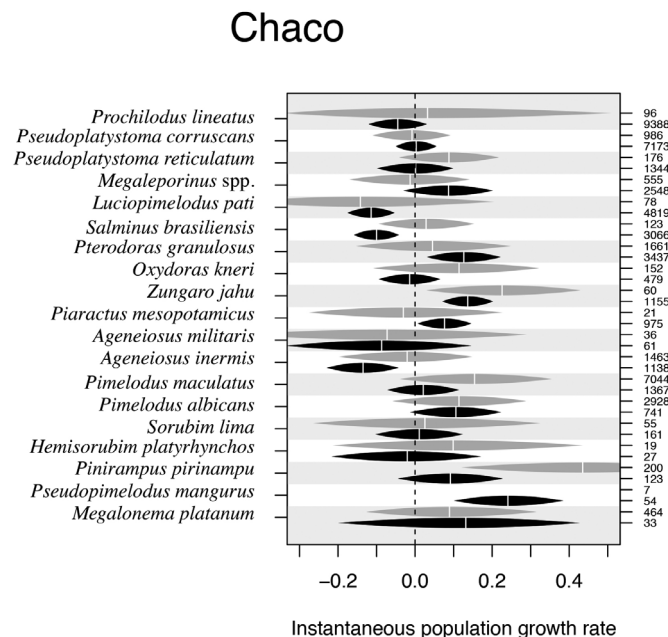


FIGURE 4 | Trends in abundance of the landings of the main 19 fish species in the commercial fishery monitoring of Chaco Province at Puerto Antequera. Ellipses represent the confidence intervals built with the maximum likelihood profile of the estimation of the instantaneous population growth rate (r). Vertical white lines within each ellipse represent the point estimate of r for each species. Black ellipses are population trends for drift gillnet landings and grey ellipses are population trends for longline landings. The dashed line at the center of the chart indicates the position of the zero value for r . Numbers on the right side of the chart are the total number of individuals caught using gillnets or longlines for each species.

Santa Fe

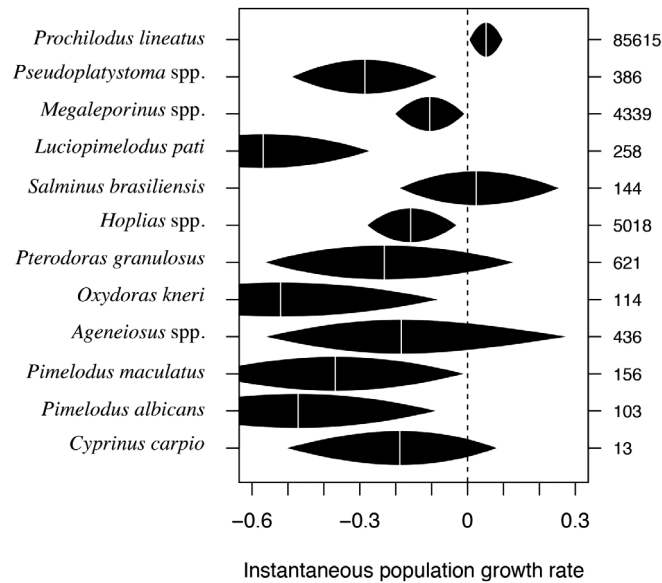


FIGURE 5 | Trends in abundance of the landings of the main 12 fish species in the commercial fishery monitoring of Santa Fe Province. Ellipses represent the confidence intervals built with the maximum likelihood profile of the estimation of the instantaneous population growth rate (r). Vertical white lines within each ellipse represent the point estimate of r for each species. The dashed line at the center of the chart indicates the position of the zero value for r . Numbers on the right side of the chart are the total number of individuals caught for each species.

Corrientes

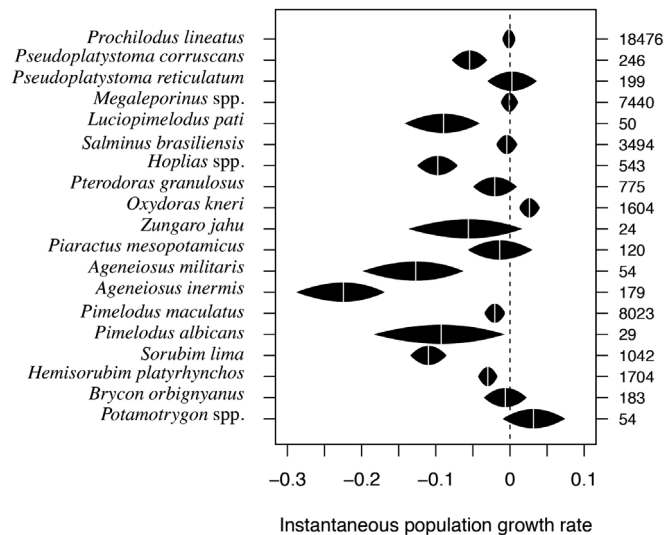


FIGURE 6 | Trends in abundance of the main 19 fish species in the survey of fish populations of EBIPES project. Ellipses represent the confidence intervals built with the maximum likelihood profile of the estimation of the instantaneous population growth rate (r). Vertical white lines within each ellipse represent the point estimate of r for each species. The dashed line at the center of the chart indicates the position of the zero value for r . Numbers on the right side of the chart are the total number of individuals caught for each species.

EBIPES

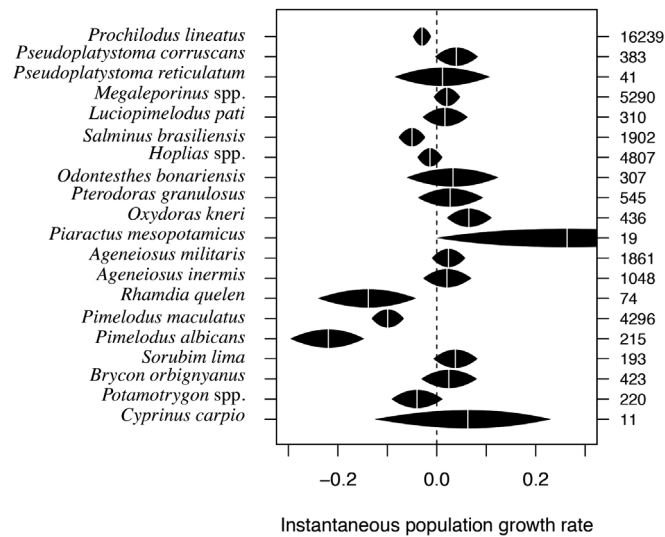


FIGURE 7 | Trends in abundance of the main 19 fish species in the survey of fish populations of Corrientes Province. Ellipses represent the confidence intervals built with the maximum likelihood profile of the estimation of the instantaneous population growth rate (r). Vertical white lines within each ellipse represent the point estimate of r for each species. The dashed line at the center of the chart indicates the position of the zero value for r . Numbers on the right side of the chart are the total number of individuals caught for each species.

The landings of the commercial fishery of Santa Fe, coming from the floodplain of the Middle Paraná River, were dominated by *P. lineatus* (88.1% of the abundance) followed by *Hoplias* spp. (5.2%) and *Megaleporinus* spp. (4.5%; Tab. 1). In this fishery, *P. lineatus* showed a positive trend; *S. brasiliensis*, *P. granulosus*, *Ageneiosus* spp., and *C. carpio* were stable or quasi-stable in the landings between April 2009 and September 2019, whereas the remaining seven species (*Pseudoplatystoma* spp., *Megaleporinus* spp., *L. pati*, *Hoplias* spp., *O. kneri*, *P. maculatus*, and *P. albicans*) had negative trends (Fig. 5). All negative and positive trends were well supported by Akaike weights (Tab. S10).

The survey of fish populations of Corrientes, located on the main channel of the Upper Paraná River between Yacyretá Dam and the confluence with the Paraguay River, was dominated by *P. lineatus* (32.7% in weight), *Megaleporinus* spp. (8.1%), and *S. brasiliensis* (7.4%; Tab. 1). Nine out of 19 species showed stable or positive trends, whereas the remaining ten species showed negative trends (Fig. 6). All negative and positive trends were well supported by Akaike weights (Tab. S11).

The fish survey of the EBIPES project, located on the floodplain of the Middle and Lower Paraná River, was dominated by *P. lineatus* (23.5% in weight), *Hoplias* spp. (10.8%) and *Megaleporinus* spp. (7.2%; Tab. 1). Fourteen out of 20 species showed stable or positive trends, whereas the remaining six species had negative trends (Fig. 7). Three of the most abundant species (*P. lineatus*, *S. brasiliensis*, and *P. maculatus*) showed negative population trends, as well as other less abundant species such as *Rhamdia quelen* (Quoy & Gaimard, 1824), *P. albicans*, and *Potamotrygon* spp. All trends were well supported by Akaike weights (Tab. S12).

Comparing the trends among databases, *P. albicans* and *P. maculatus* had negative trends in both surveys of fish populations (EBIPES and Corrientes) and also in the landings of Santa Fe Province, but showed stable or increasing trends in the fishery monitoring of Chaco. Similarly, *Potamotrygon* spp. had a declining trend in the Middle Paraná (EBIPES survey), but an increasing trend in the Upper Paraná (Corrientes survey). *Hoplias* spp. had negative trends in two out of the three surveys in which it was included, both in the Middle and Upper Paraná River (Santa Fe and Corrientes). In the survey of fish populations of EBIPES, its trend was stable but with a tendency to be negative (Fig. 7). *Salminus brasiliensis* had negative trends both in the EBIPES survey and Chaco monitoring (only for drift nets). *Luciopimelodus pati* and *Ageneiosus* spp. had negative trends in the commercial fishery monitoring of Santa Fe and Chaco and also in the survey of fish populations of Corrientes. None of the 12 shared species among the four databases, showed negative trends in all analyses.

Other species had coincident stable or positive trends in more than one dataset. *Megaleporinus* spp. had positive or stable trends in Chaco, Corrientes and EBIPES, but a declining trend in the Santa Fe monitoring. The Doradid catfishes *P. granulatus* and *O. kneri* were stable or increasing in all datasets, except for *O. kneri* in the Santa Fe monitoring. The size of the confidence intervals of the surveys of fish populations of EBIPES and Corrientes, were generally smaller than the confidence intervals of the commercial fishing monitoring of Santa Fe and Chaco, indicating more reliable estimates of the trends in the abundance of each species.

DISCUSSION

This study is the first comprehensive analysis on the historical trends in the fishery landings of the Lower La Plata basin including the evaluation of the 21 most frequent fish taxa in commercial fisheries between 1934 and 2019. Fishing statistics for species under exploitation in the Argentine sector of the La Plata basin are compiled for the first time in a spatio-temporally comprehensive scale. Previous studies have analyzed the temporal trends of most important species (Quirós, Cuch, 1989), including only a portion of the rivers of the basin (Fuentes, Quirós, 1988), or representative landing sites (Rabuffetti *et al.*, 2017; 2020), or excluding most of industrial fishing (Quirós, 1990) which hindered the observation of the global trends of the landings of each species in southern La Plata basin. The availability of the historical trends in the exploitation of each species is useful to put in context the current exploitation levels of each species and have been used to establish cautionary criteria when little fishery information is available (Espinach Ros, Sánchez, 2007). We also present for the first time an analysis estimating the recent population trends for 27 commercial fish species from fisheries monitoring and fish population surveys.

The main species of the fishery of the Lower La Plata basin, such as *Prochilodus lineatus*, *Megaleporinus obtusidens*, *Salminus brasiliensis*, *Pseudoplatystoma corruscans*, *Pseudoplatystoma reticulatum* Eigenmann & Eigenmann, 1889, and *Luciopimelodus pati*, are migratory species which exhibit life history traits coincident with a periodic strategy (*sensu* Winemiller, 2005). These species have high longevity, long generation times, and high fecundity, with small eggs that are released into the river without parental

care (reviewed in Abrial *et al.*, 2019; but see Balboni *et al.*, 2021 for data on *P. corruscans*). Spawning and larval flow are closely linked to the variations in the hydrometric level (Fuentes, Espinach Ros, 1998) and the survival of juveniles strongly depends on the presence of large and long-standing floods in coincidence with the warm periods of the year (Winemiller, 2004; Bailly *et al.*, 2008; Espinach Ros *et al.*, 2012). In *Prochilodus lineatus* for example, the high longevity and the successful episodic recruitment separated by several years, determine that the replacement of one successful cohort by another can take more than a decade (Espinach Ros *et al.*, 2012). These episodic recruitment pulses generate continuous population fluctuations in relation to fluctuations in the environmental conditions of the system over long temporal scales (Quirós, Cuch, 1989; Rabuffetti *et al.*, 2017). Part of the slight declines and increases observed in some databases (spanning between 9 and 15 years in EBIPES, Santa Fe and Chaco monitorings) can be associated with population fluctuations inherent to this strategy, mainly in the databases of the surveys of fish populations where the abundance data includes both adult and juveniles (because of inclusion of both small and large mesh sizes) and mainly in environments of the floodplain of the Lower and Middle Paraná River, recognized as nursery habitats for migratory species (Scarabotti *et al.*, 2011).

The exploitation of *Prochilodus lineatus*, the dominant species of the fishery, gradually decreased between 1934 and 1986 in all rivers combined of the Lower La Plata basin (Fig. 2), mainly in association with the decrease and subsequent prohibition of industrial fishing for fish meal and oil during the period. Landings of *P. lineatus* decreased in the Uruguay, La Plata and Lower Paraná rivers where all industrial fishing was carried out, while increased in the Middle Paraná and Upper Paraná, where landings are destined for human consumption. Using the same database, Quirós (1990) observed an increase in the landings of *P. lineatus* for the period 1945–1986, but excluded from the analysis the two most important landing sites for industrial fishing (Tigre, at the end of the Paraná River Delta; and Galeguaychú, in the Lower Uruguay River), describing mainly the patterns of the landings for human consumption. Between 1994 and 2004, the increase in exploitation was associated to the boom in exports as a result of international market demands (Iwaszkiw, Lacoste, 2011; Baigún *et al.*, 2013), where a peak of 37597 t was reached, which almost tripled the historical maximum extraction values for this species (Fig. S5). Between 2005 and 2007, the national government applied quotas (National Law 26292; Resolution 2/2007 — and subsequent resolutions — of the Ministry of Economy and Production of Argentina) which reduced exports for some years. However, landings increased steadily since 2008 and currently, they exceed historical values again. These regulations were also applied to other species such as *Megaleporinus* spp. and *Hoplias* spp., whose trends in exports followed a similar pattern.

Current population trends of *Prochilodus lineatus* are stable in the commercial fisheries of Santa Fe and the survey of fish populations of Corrientes but showed a slight decline in the abundance in the Middle and Lower Paraná in the EBIPES monitoring program and a slight trend to decline in the northern end of the Middle Paraná River, in Chaco. Fishery statistics of *P. lineatus* taken during the last 15 years in the lower La Plata basin indicate a low total mortality rate, and size structures that fluctuate mainly as a result of episodic recruitment phenomena (Espinach Ros *et al.*, 2012; CARP *et al.*, 2012; 2016; Liotta *et al.*, 2020). These statistics showed 13-year-old cohorts that sustained the fishery in 2010 and persisted during the period of greatest exploitation rate observed between

2003 and 2006, indicating moderate exploitation rates for the species. A recent fishery assessment (Baigún *et al.*, 2013) suggested that *Prochilodus lineatus* could have been fully exploited or even overexploited in the recent past and reported a reduction in body size. However, this study overestimated mortality rates more than twice from those observed empirically by Espinach Ros *et al.* (2012) and calculated the relationship between productivity and yield only for 21% of the area of the Paraná River floodplain and delta, where most of the commercial exploitation of the species occurs. Studies on the age structure of the populations of *P. lineatus* using otoliths detected superabundant cohorts that coincide with the extraordinary floods observed during the last 25 years (e.g., 1997, 2007, 2010, 2016) in the Paraná River (Espinach Ros *et al.*, 2012; Liotta *et al.*, 2020). The negative trend of the EBIPES database, which started in 2005, could be explained by the events of extraordinary recruitment of 2007 and 2010, which registered a greater abundance of juveniles than the event of 2016 (Lozano *et al.*, 2019). In terms of weight, the EBIPES catches between 2006 and 2019 show a stable trend (Liotta *et al.*, 2020). The stability of the populations of *Prochilodus lineatus* observed in Corrientes database, with a longer sampling period (27 years) and a lower impact of the recruitment episodes in this main channel environment, supports this hypothesis.

The landings of the herbivorous and omnivorous species *P. mesopotamicus* and *Brycon orbignyanus* (Valenciennes, 1850) and the euryhaline anadromous species such as *O. bonariensis* and *Lycengraulis grossidens* (Spix & Agassiz, 1829) declined during the period 1934–1986, mainly in the Río de la Plata and the Lower Paraná River. In these species a very similar pattern of decline in the landings is observed, with a more or less abrupt decline from the mid-1970s, which is also followed by *Z. jahu* (Figs. S1 and S4). On one hand, *P. mesopotamicus*, *B. orbignyanus* and *Z. jahu* were captured in the Lower Paraná and Río de la Plata, until the 1970s (Lahille, 1906; MacDonagh, 1937; Vidal, 1969), but today they have completely disappeared from the landings in these reaches, and their landings are currently limited to the upper end of the Middle Paraná and Paraguay River (Petriere Jr *et al.*, 2002; Vargas, 2020). On the other hand, *O. bonariensis* and *L. grossidens* were distributed throughout the Middle Paraná River up to Corrientes (Ringuelet *et al.*, 1967) and were captured in abundance in the Río de la Plata and Lower Paraná River (Fig. S1), but landings are currently low (*O. bonariensis*) or non-existent (*L. grossidens*) (Baigún *et al.*, 2003). Although *O. bonariensis* showed an increasing trend in national exports, its current abundance in the Río de la Plata is very low (CARP *et al.*, 2012; 2016) and these catches would come from fishing in shallow Pampasic lakes where it represents one of the most abundant species (Mancini *et al.*, 2016). The highest historical landings of *O. bonariensis* and *L. grossidens* occurred during 1940s and 1950s respectively, and remained in lower values during the two or three following decades (Fig. S1), indicating that the decline that suffered these species after the 1970s occurred several decades after the maximum exploitation rates observed in of these species. For other anadromous species entering the Río de la Plata, such as *Genidens barbatus* (Lacepède, 1803), the occurrence of the flood pulse in phase with the reproductive season is a key determinant of fish abundance (Vidal *et al.*, 2021). In this sense, Quirós (1990) linked the decline of anadromous fish landings in the Paraná River during the 1970s to the changes in the hydrological regime induced by the great hydropower development in the upper basin in Brazil, which altered the flood regime of the middle and lower Paraná River.

The past decline in the landings of *P. mesopotamicus*, *B. orbignyanus* and *Z. jahu* has

been associated to the river regulation and deforestation in the upper Paraná River basin (Bonetto *et al.*, 1989; Quirós, 1990). River regulation, deforestation and changes in rainfall patterns in the upper Paraná River brought profound changes in the hydrological regime of the lower reaches, such as the reduction in the amplitude of the water level fluctuations, the elevation of the minimum water levels and the loss in the regularity and seasonality of the floods (Quirós, 2004; Lee *et al.*, 2018), which can affect fish seasonal migrations and reproduction (Bonetto *et al.*, 1989; Rabuffetti *et al.*, 2020). Deforestation is the main factor explaining the increases in river discharge of the Paraná River since 1970, whereas changes in the rainfall patterns as a product of climate change explained the delay in the onset of the seasonal flooding (Lee *et al.*, 2018). Bonetto *et al.* (1989) suggested that the extensive deforestation suffered by the Atlantic and gallery forests, reduced the entry of allochthonous material such as fruits and seeds and determined the decline of herbivorous species like *P. mesopotamicus* and *B. orbygnianus*. Deforestation has been linked to the decline in the landings of other neotropical inland fisheries (Barletta *et al.*, 2010; Barros *et al.*, 2020). In addition, the loss of seasonality in floods could limit the access to the seasonal resources such as fruits and seeds of terrestrial plants that fall into the water during floods in late summer. In the upper Paraguay River, where a natural hydrometric regime and riverine forests are still conserved, *P. mesopotamicus*, *B. orbygnianus*, and *Z. jahu* are important in the commercial and recreational catches (Petrere Jr *et al.*, 2002). Overfishing cannot be completely ruled out as another driver of the retraction of these species to the north, as they disappeared progressively from areas of high (south) to lower fishing effort (north). In contrast with the past declines in the landings of these species, current population trends of *P. mesopotamicus*, *B. orbygnianus*, and *Z. jahu* showed stability or increase (with the exception of *Z. jahu* in the upper Paraná in Corrientes, which was evaluated with few individuals), indicating that current threats (*e.g.*, fishing and environmental alterations) would not be generating additional declines of these species at present.

Ten out of the 11 species that declined in the database of Corrientes, in a reach of the Upper Paraná River downstream from the Yacyretá dam, were Siluriforms. Siluriform species are widely recognized to prefer turbid environments because they are mainly non-visual species that rely on turbid conditions for prey capture and predator avoidance (Rodríguez, Lewis Jr., 1997; Pouilly, Rodríguez, 2004; Scarabotti *et al.*, 2011). From the 1990s, water transparency of the Upper Paraná River at Corrientes has been increasing significantly due to a reduction to less than one fifth (18%) of the historical average sediment load due to sediment retention by dams installed in the upper basin (Amsler *et al.*, 2007). These changes also determined a reduction in the amount of nutrients, mainly phosphorus (Nogueira *et al.*, 2021), leading to an oligotrophic state that probably disrupted some food chains integrated by fish (*e.g.*, Santana *et al.*, 2017). Then, the generalized decline of Siluriform species in the Upper Paraná River, from 1994 to date could be partially explained by selective mortality or emigration induced by the increase in water transparency. The suspended sediment load of the Middle and Lower Paraná River has remained near their historical values, as a result of the increased supply of sediments due to the increase in erosion rate in the by Bermejo River Basin (Amsler *et al.*, 2007). In this sector, only three out of the seven species that declined in the EBIPES database were Siluriforms. The relationship between the decline of Siluriforms and the increase of the transparency is a plausible hypothesis that should be addressed in future

studies.

Medium-sized catfishes such as *P. albicans*, *P. maculatus*, and *R. quelen* had negative trends in almost all monitoring programs. The commercial exploitation of *P. maculatus* and *P. albicans* increased steadily until 1986, but there is sparse information on exploitation rate at the present. Cleminson (2000) observed steady trends in catches of *P. maculatus* in sport fishing tournaments between 1973 and 1997. Both species were the most abundant in longline landings of Puerto Antequera. In the Middle Paraná River, *P. maculatus* is the species most frequently caught by recreational fishermen, generally without release (del Barco, 2008). The Santa Fe Province has an estimated number of 300000 recreational fishermen (Cleminson, 2000), that can be projected to 500000 for all the Middle and Lower Paraná River, suggesting that these species could be declining because of a combined effect of both commercial and recreational fishing pressure.

From 1934 to 1986, *S. brasiliensis* showed a negative trend in commercial landings in almost all the rivers in the basin. Fuentes, Quirós (1988) associate the decline of this species since the 1950s to the low hydrometric levels of the Paraná River and to the application of partial closures during the reproductive season in the period 1961–1969. Due to its aesthetic, fighting and size attributes, *S. brasiliensis* is considered one of the most valued sport fish species in the La Plata basin and has motivated the development of a high-priced, international-quality recreational fishery oriented towards trophy size fish or high daily catch (Vigliano *et al.*, 2010). Starting in the 1970s, the pressure of the sport fishing industry determined the application of total bans for the commercial catch of this species, mainly in Upper and Middle Paraná, which generated a reduction in the reports of *S. brasiliensis* in most landing points, although illegal trade continued (Fuentes, Quirós, 1988). The current trends of the species show a decrease in the catches of the Middle Paraná (EBIPES dataset) and in Chaco (only for drift gillnets), but it is stable in the longline catches of Chaco and the gillnet catches in Santa Fe (this value should be taken with caution due to the bans for this species in this fishery and because the assessment was carried out on the basis of few individuals). These trends in the Paraná River could be explained by the great fishing and commercial pressure on the Middle Paraná River and by the lower compliance with the protection measures. Alternatively, considering that the time span of EBIPES and Chaco programs are similar, the population decline could be also related to the higher frequency of recruitment events at the beginning of these monitoring programs, as was mentioned for *Prochilodus lineatus*. The stability of the catches in Corrientes can be related to the longer time span of this database and with the strong protection and control measures in the upper basin where catch-and-release sport fishing predominates (Espinach Ros, Fuentes, 2000; Vigliano *et al.*, 2010).

The most important large predatory catfishes in the fishery, *Pseudoplatystoma* spp., and *L. pati* showed a great concordance in the landing patterns during the period 1934–1986 (Fig. S1), with slight declines in the lower part of the basin (Uruguay River and Río de la Plata), but with sustained increases in the rest of the landing sites in the middle and upper reaches of the basin. Fuentes, Quirós (1988) attribute this increase to the replacement of *S. brasiliensis* by *Pseudoplatystoma* spp. in commercial fishing for high-valued fish, due to the bans on *S. brasiliensis* mentioned above. These regulations probably impacted on the landings of *L. pati*, a less valued species in the market, which is caught with the same gears that *Pseudoplatystoma* spp. (Bechara *et al.*, 2007; Vargas, 2020). Despite their large size and high trophic level, these species continue to be important

in the fishery today, mainly in the upper portion of the Middle Paraná (Vargas, 2020) although reductions in body sizes with respect to the past have been detected (Quirós, 1990; Quirós *et al.*, 2007). At present, the populations of these species show stable trends in the Middle Paraná River, but during the last 27 years they showed a decline in the upper Paraná, probably due to the change in habitat conditions mentioned above, and the reduction of its breeding area caused by the installation of dams in the Upper Paraná River (Oldani *et al.*, 2007).

Hoplias spp. showed population declines in the surveys of fish populations of both the Middle Paraná and the Upper Paraná River and in the commercial fishery monitoring of Santa Fe. Comparing current exports with historical landings, *Hoplias* species have experienced a spectacular 11.6-fold increase in fishing exploitation since 1994, which may even be underestimated considering that exports do not include the domestic market. Due to its relatively low fecundity, the investment of energy in parental care and the absence of migrations, *Hoplias* spp. can be classified within a life history strategy intermediate between equilibrium and periodic (reviewed in Abrial *et al.*, 2019). Equilibrium species tend to have slower recovery rates to fishing exploitation than periodic species and require stable environments for their reproduction (Winemiller, 2005). For this reason, it is expected that *Hoplias* species could be declining in response to the high fishing pressure. Traditionally, only one species of *Hoplias* was recognized in the La Plata basin, but recently at least five species of *Hoplias* have been identified in the Lower La Plata basin (Cardoso *et al.*, 2018; Rosso *et al.*, 2018; Mirande, Koerber, 2020). Fishery biologists should make an effort to differentiate these species in landing monitorings to have independent statistics for each species. Also, life history studies should be revised, as they probably included individuals of different species. Finally, it is necessary to evaluate the sustainability of the fisheries targeting *Hoplias* species because of the generalized use of small mesh sizes (around 10 cm between opposite knots) which can capture a large portion of the juveniles of the large migratory species that coexist in the same environments.

Megaleporinus spp. also showed a large increase in the fish exports from 1994 to the present, but populations remain stable or increasing in all databases with the exception of Santa Fe fishery. On one hand, the stability or slight increase in populations observed in this study could be due to the reduction in fishing pressure by the establishment of quotas for exports from 2013. However, this species is highly commercialized in the domestic market due to the quality of its meat, and fishing pressure could continue despite the limitation of exports. On the other hand, *Megaleporinus* spp. are the main consumers of the invasive golden mussel *Limnoperna fortunei* (Dunker, 1857) which tend to dominate among the trophic items of the species (Montalto *et al.*, 1999; García, Protogino, 2005). Sylvester *et al.* (2007) demonstrated that fish predators can consume between 25 and 79% of the enormous mussel productivity of the Paraná River, and suggested that *L. fortunei* intercepts a significant fraction of the organic carbon that the rivers of the La Plata basin flush into the ocean, increasing the productivity of invertivorous animals. In fact, stable isotope analysis indicated that *L. fortunei* is the main energetic source of *Megaleporinus* spp. in the Uruguay River (González-Bergonzoni *et al.*, 2020), which evidences a strong change in resource use in a fish formerly classified as herbivorous (López-Rodríguez *et al.*, 2019). Boltovskoy, Correa (2015) suggested that the great environmental abundance of this mollusk could represent a notable increase

in resource availability, promoting the population growth of *Megaleporinus* species. These processes may also explain the stable or positive trend of the Doradid catfishes *P. granulatus* and *O. kneri*. These species are also omnivorous and their predation on *L. fortunei* has also been recorded (Montalto *et al.*, 1999).

The exotic common carp *C. carpio* showed negative population trends in the fisheries of Santa Fe and a stable trend in the EBIPES survey. This species was first introduced in Argentina in the mid-nineteenth century for ornamental and aquaculture purposes, and was recorded for the first time in the wild in the Río de la Plata in 1945 (MacDonagh, 1945; Baigún, Quirós, 1985), and currently it is present in the commercial fisheries at the southern end of La Plata basin. In recent decades, the species has notably expanded its distribution in Pampasic lakes, streams and rivers, where it becomes predominant, and has spread to all of northern Argentina (Maiztegui *et al.*, 2016). In the inner portion of the Río de la Plata, the abundance of *C. carpio* oscillates around 10% of the biomass (García *et al.*, 2010; CARP *et al.*, 2012; 2016), and it is more abundant near Buenos Aires city, where it reaches up to 50% of the biomass (CARP *et al.*, 2016). However, in our study *C. carpio* represented only 0.08% of the biomass in the Middle Paraná River (EBIPES and Santa Fe fishery), and was absent in the Chaco fishery and the Upper Paraná River downstream Yacyretá Dam. *Cyprinus carpio* accounts only for 1% of the landings in a channel fishery in the Lower Paraná River (Liotta, 2020). In the Paraná River, the population growth of *C. carpio* would be limited by the combined effect of species richness, the functional saturation of assemblages, and predation pressure of native species (Maiztegui *et al.*, 2016).

Stingrays, *Potamotrygon* spp., tended to increase in the Upper Paraná River, and decreased in the Middle Paraná River. Population trends of *Potamotrygon* species were analyzed for the middle Paraná River by Lucifora *et al.* (2017). In this reach the declining group included mainly the giant stingray *Potamotrygon brachyura* (Günther, 1880), while the ocellated species group, composed mainly of *Potamotrygon motoro* (Müller & Henle, 1841), remained stable (Lucifora *et al.*, 2017). Large-bodied species such as *P. brachyura* has also a much lower maximum rate of population increase than *P. motoro*, which renders it more prone to population declines than *P. motoro* (LOL, PAS, SAB, work in progress). In the Upper Paraná, *P. brachyura* appears to be relatively less common than in the Middle Paraná, according to recreational fisheries records (Lucifora *et al.*, 2015) and the Corrientes fish survey data. The lower relative importance of *P. brachyura* (a low productive species) and the higher relative importance of *P. motoro* (a high productive species) in the Upper Paraná may explain why the trend for *Potamotrygon* spp. in this area is increasing. The converse is true for the Middle Paraná River, where the relative importance of *P. brachyura* is higher. Alternatively, the difference in trends can also be explained with a similar species composition between areas, if fishing pressure on *P. brachyura* is higher in the Middle Paraná than in the Upper Paraná.

In general, the situation found in the lower Plata basin by our study is one of a multispecies fishery with declines in a fraction of the species that compose the fishery. The good news is that compared with other large tropical and subtropical rivers of the world affected by large-scale fisheries and strong basin development (*e.g.*, Upper Paraná, Mekong, Yangtze), the lower La Plata basin fish populations are in better shape. In the lower La Plata Basin, no fish species has gone extinct regionally or globally, and the number of big dams blocking fish migrations is still low in comparison with the Upper

Paraná River. This means that there is still room to reach sustainable levels of exploitation and recover declining and retracting species. Fisheries management must not only make decisions about the regulation of fishing effort, but also agree on an ecosystem approach for inland fisheries (Baigún *et al.*, 2008; Beard *et al.*, 2011) with the different users of the system, where the ecological, social and economic spheres are balanced. Clearly, national and provincial authorities, as well as supra-national government bodies (*e.g.*, CARU, Comisión Mixta del Río Paraná, CARP) have an opportunity for sustainable fisheries by supporting fishery and basin managers to apply science-based management. It is their responsibility not to miss this opportunity.

ACKNOWLEDGMENTS

We thank the many people that participated in the fisheries monitoring and fish population surveys along the past three decades collecting the information used in this work. We also thank the librarians of the Instituto Nacional de Investigación y Desarrollo Pesquero of Argentina (INIDEP) to provide access to the digital collection of the continental fishery statistics of Argentina. Two anonymous reviewers provided insightful comments on an early version of the manuscript, that greatly improved the quality of the study. This work has been funded by the Agencia Nacional de Promoción Científica y Tecnológica [grant PICT 2018-1478], from Argentina.

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ETHICAL STATEMENT

All sampling was carried out by provincial and national authorities, with the corresponding authorizations and following local regulations (Law 12212, for Santa Fe Province; Law 5628, Decree 422/2010, Art. 35, for Chaco Province; Authorization of the Directorate of Natural Resources, for Corrientes survey, and Resolution XIII/N°9/2004 and XVII/N°5/2007 CFA, for EBIPEs survey).

COMPETING INTERESTS

The authors declare no competing interests.

HOW TO CITE THIS ARTICLE

- **Scarabotti PA, Lucifora LO, Espínola LA, Rabuffetti AP, Liotta J, Mantinian JE, Roux JP, Silva N, Balboni L, Vargas F, Demonte LD, Sánchez S.** Long-term trends of fishery landings and target fish populations in the lower La Plata basin. *Neotrop Ichthyol.* 2021; 19(3):e210013. <https://doi.org/10.1590/1982-0224-2021-0013>

Neotropical Ichthyology



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Official Journal of the Sociedade Brasileira de Ictiologia