Biological Conservation 210 (2017) 293–298

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Decline or stability of obligate freshwater elasmobranchs following high fishing pressure

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ARTICLE INFO

Keywords:
Chondrichthyes
Overfishing
Potamotrygon
South America
Wetlands
Fishery management

ABSTRACT

Despite elasmobranchs are a predominantly marine taxon, several species of sharks and rays are regularly found in fresh water. Although there is ample evidence of declining elasmobranch populations around the world, this evidence comes exclusively from marine and euryhaline species; the ecology and conservation status of obligate freshwater elasmobranchs is far from being understood. River stingrays (Potamotrygoninae, 32 species) live exclusively in South American rivers and represent the overwhelming majority of freshwater elasmobranch diversity. Here, we present evidence of a decline in the abundance of river stingrays in the middle and lower Paraná River, an extensive wetland mosaic of approximately 35,000 km^2. By taking advantage of a stingray-manipulation procedure widespread among South American fishermen, we were able to estimate spatial differences in relative fishing pressure and found that the observed decline is related to fishing pressure. The highest fishing effort and lowest relative abundance occurred in areas where fisheries operate on the river floodplain. The lowest fishing effort and highest relative abundances occurred in areas where fisheries operate in the main channel. The only species with a stable trend was *Potamotrygon motoro*. This evidence confirms the long-presumed vulnerability of obligate freshwater elasmobranchs and suggests that some species, *e.g. P. motoro*, can be exploited sustainably. Our results also indicate that negative effects on freshwater elasmobranchs can be minimized by adjusting fishing grounds.

1. Introduction

In recent years, the evidence that shark and ray populations around the world are declining has been growing (Baum et al., 2003; Ferretti et al., 2008; Field et al., 2009; Dulvy et al., 2014). In most cases, these declines are the result of overexploitation. Overfishing is the most important threat to marine elasmobranchs, because they have naturally low intrinsic population growth rates (Field et al., 2009), therefore even moderate levels of fishing effort may be enough to negatively affect a population of a given elasmobranch species (Myers and Worm, 2005). All of this evidence comes from marine species, and very little information on the status of freshwater elasmobranchs is available.

Sharks and rays live mostly in marine environments, but approximately 60 species (5%) of elasmobranchs occur in freshwater environments. Some species, termed euryhaline elasmobranchs, are marine species that have the physiological ability to enter, survive for extended periods, and even reproduce in freshwater environments. Obligate freshwater elasmobranchs, on the other hand, are species that complete their entire life cycle in fresh water and cannot survive in sea water (Lucifora et al., 2015). Most of the world's obligate freshwater

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http://dx.doi.org/10.1016/j.biocon.2017.04.028
Received 14 December 2016; Received in revised form 17 April 2017; Accepted 24 April 2017
0006-3207/

elasmobranch diversity is contained in a single clade, the subfamily Potamotrygoninae, which is endemic to tropical and subtropical rivers and wetlands of South America, east of the Andes. This lineage is unique among extant elasmobranchs in that it radiated exclusively in fresh water from a marine ancestor (Rosa et al., 2010; Lucifora et al., 2015).

Freshwater elasmobranchs are thought to be highly susceptible to human threats, but no evidence on actual population trends has ever been presented. Obligate freshwater elasmobranchs combine the high intrinsic vulnerability to anthropogenic threats typical of marine elasmobranchs with living in a small habitat (as compared to the ocean) that is highly impacted by growing human populations (Compagno and Cook, 1995; Rosa et al., 2010; Dulvy et al., 2014; Lucifora et al., 2015). This makes obligate freshwater elasmobranchs vulnerable to both habitat degradation and, similar to their marine relatives, overfishing (Compagno and Cook, 1995; Rosa et al., 2010; Dulvy et al., 2014; Lucifora et al., 2015). Furthermore, while distant populations of euryhaline elasmobranchs can be linked by individuals dispersing through marine environments (Li et al., 2015), populations of obligate freshwater elasmobranchs are more limited in their dispersal possibilities (Compagno and Cook, 1995). Despite this presumed susceptibility of obligate freshwater elasmobranchs to anthropogenic threats, little scientific knowledge is available on their biology and ecology as to allow for a sound assessment of their actual conservation status (Compagno and Cook, 1995; Rosa et al., 2010; Dulvy et al., 2014; Lucifora et al., 2015). As a result, 54.5% of all obligate freshwater elasmobranchs are categorized as Data Deficient by the International Union for Conservation of Nature and Natural Resources (IUCN) (Dulvy et al., 2014).

The Paraná River, within the Río de la Plata basin, is a major river in South America, second in length only to the Amazon. It runs for almost 4000 km in a general north-south direction through Brazil, Paraguay and Argentina (Bonetto, 1986). After receiving the Paraguay River, where its middle reach begins, the Paraná forms a large, complex floodplain composed of secondary channels, islands, bars, shallow lakes and swamps (Paira and Drago, 2007) (Fig. 1). This floodplain expands laterally and forms an extensive delta in its lower reach (Bonetto, 1986) (Fig. 1). Together, the middle and lower reaches of the Paraná River comprise a subtropical wetland mosaic of approximately 35,000 km^2, that ends in the Río de la Plata, between Argentina and Uruguay (Bonetto, 1986; Paira and Drago, 2007).

Six species of river stingrays of the genus *Potamotrygon* occur in the middle and lower Paraná River: *P. amandae*, *P. brachyura*, *P. falkneri*, *P. histrix*, *P. motoro*, and *P. schuhmacheri* (Rosa et al., 2010; da Silva and de Carvalho, 2011; Loboda and de Carvalho, 2013; Lucifora et al., 2016). Five of these species are categorized as Data Deficient by the IUCN (Charvet-Almeida and de Almeida, 2004; Drioli and Chiaramonte, 2005; de Araújo, 2009; Charvet-Almeida et al., 2009; Soto et al., 2009), and *P. amandae* has not been assessed. Some of these species are of particular conservation concern because they have traits that correlate positively with high extinction risk, such as endemicity, large body size and rarity (Pimm and Jenkins, 2010; Dulvy et al., 2014). Four species (*P. amandae*, *P. brachyura*, *P. histrix* and *P. schuhmacheri*) are endemic to the Río de la Plata basin (Rosa et al., 2010; Loboda and de Carvalho, 2013; Lucifora et al., 2016). *P. brachyura* attains a very large body size, reportedly exceeding 200 kg (Lucifora et al., 2016), and *P. schuhmacheri* is one of the rarest elasmobranch species (either freshwater or marine), since it is known from less than 5 specimens (Rosa et al., 2010).

Stingray tail mutilation is an extended practice along the Paraná River (*e.g.* Castex, 1963; Garrone Neto, 2010), as well as in many other South American rivers (*e.g.* Rincon, 2006; Duncan et al., 2010; Oddone et al., 2012; Gama and Rosa, 2013; Rincon et al., 2013). When fishermen catch a river stingray, it is very common that they cut off its tail just anterior to the sting (Rosa et al., 2010). This practice has the objective of eliminating the possibility of being stung by the stingray, ensuring a safe manipulation of the catch. Many stingrays that are returned to the water after having their tail cut survive since, in some areas, it is common to catch stingrays with cut, healed tails (Rosa et al., 2010). It has been shown that, in a tributary of the Tocantins River (Brazil), tailless stingrays are far more common around fishing villages than in river reaches far away from human settlements (Rincon, 2006). Therefore, the incidence of tailless stingrays in a given area can be taken as a proxy for fishing pressure.

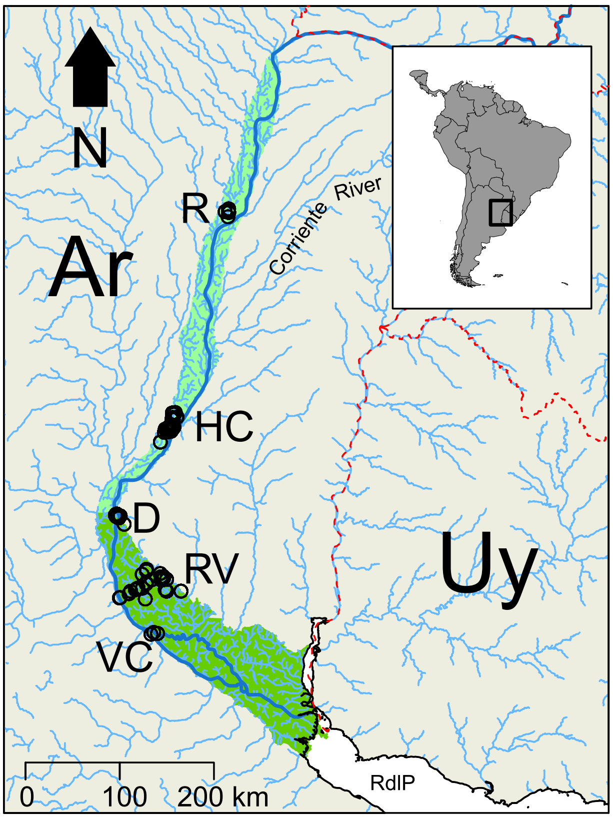

Fig. 1. Map of the middle and lower Paraná River, showing study area and sampling localities. Places where samples were taken (empty circles) are grouped in locations identified with capital letters (R: Reconquista, HC: Helvecia/Cayastá, D: Diamante, RV: Rosario/Victoria, VC: Villa Constitución). The middle Paraná River floodplain is shaded in light green, and the lower Paraná River floodplain and delta is shaded in bright green. The main channel of the Paraná River is shown in bold blue. The inset shows the location of the study area in South America. Ar: Argentina; Uy: Uruguay; RdlP: Río de la Plata. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Here, we present the first formal assessment of abundance trends for obligate freshwater elasmobranchs and evaluate the relationship between the observed trend and fishing pressure by utilising a manipulation technique (*i.e.* tail mutilation) that is widespread among South American fishermen.

2. Materials and methods

2.1. Sampling

Samples came from a standardised sampling program conducted by the project "*Evaluación Biológica y Pesquera de Especies de Interés Deportivo y Comercial en el Río Paraná, Argentina*" (Biological and Fishery Assessment of Recreational and Commercial Species of the Paraná River, Argentina). This program samples regularly at different sites along the middle and lower Paraná River (Fig. 1) using, at each site, batteries of gillnets and trammel nets of different mesh sizes to catch a representative sample of species and sizes. Gillnet batteries consisted of 25-m long pannels with mesh sizes of 30, 40, 50, 60, 70, 80, 90, 105, 120, 140, 160, and 180 mm between opposed knots. Trammel nets were also 25 m in length, and had outer pannels of 240 mm between opposed knots, with inner pannels of 105, 120, 140 or 160 mm between opposed knots. All gillnets and trammel nets were made of multifilament nylon strings, except the 90-mm gillnet which was made of monofilament nylon strings. Between 2005 and 2016, locations were regularly sampled four times a year in different seasons, covering the full range of temporal variation in environmental factors. Gillnets and trammel nets were set at dusk, left overnight, and hauled at dawn, for an average soak time of 12 h. While the arrangement of nets sometimes varied depending on local conditions, they were set at least 300 m apart of each other to avoid interference among them. All sampling was carried out in accordance with provincial and federal regulations.

2.2. *Temporal trends*

Sets of net batteries at a given site and date were taken as sample units (n = 429). Sampling effort (*ef*) was taken as the number of nets set at each site and date. For each sample unit, the following data were taken: date (D), year (Y), latitude (L), location (Lo), hydrometric level (H), number of stingrays caught (N), and number of individuals of *P. motoro* caught (N_{Pm}). Date was transformed to consecutive day for each year (D), with January 1st being day 1 and December 31st being day 365, and transformed to sine and cosine to represent a seasonal cycle.

Species-specific identification was not always possible, especially during the early surveys of the sampling program. Starting in 2011, stingrays caught during the sampling program were kept in the permanent collection of the *Instituto de Biología Subtropical – Iguazú* (IBSI). Using specimens stored in the IBSI collection we were able to compare the species identification of individuals in the database with their actual species identity. We found that *P. motoro* was the only species that was reasonably well identified. Three species of the *P. motoro* species complex occur in the Paraná River basin: the true *Potamotrygon motoro*, *P. amandae* and *P. pantanensis* (Loboda and de Carvalho, 2013). Based on the examination of 37 specimens, we could determine that all true *P. motoro, i.e. P. motoro* as differentiated from *P. amandae* and *P. pantanensis* by Loboda and de Carvalho (2013), were identified as such in the database, and that 9.25% of the individuals identified as *P. motoro* in the database were actually another species (always *P. amandae*). All other species were either identified as *Potamotrygon* sp. or misidentified as a different species, but not in a consistent way. Therefore, we were able to conduct three different analyses: One for all species of *Potamotrygon* pooled together, another for *P. motoro*, and a third one for the genus *Potamotrygon* excluding *P. motoro*.

Data were used to build generalized linear models (GLM). The number of individuals of *Potamotrygon* (N_{Po}), of *P. motoro* (N_{Pm}), and of *Potamotrygon* excluding *P. motoro* (N_{Pspp}) were used as dependent variables. The three analyses were based on 361, 171, and 190 stingray individuals, respectively. For each dependent variable, two sets of models were run, since L and Lo were correlated and could not be included in the same model. One set included Y, L, H, and D, and the other included Y, Lo, H, and D. Both sets included log(*ef*) as an offset term, a negative binomial error structure and a log link (Baum et al., 2003; Ferretti et al., 2008). A negative binomial distribution was applied because the dataset had a large number of zeroes making the variance much greater than the mean, and the response variable was discrete. For each set of models, a stepwise procedure was applied in which a variable was taken out of the model and the Akaike Information Criterion (AIC) was calculated. The model with the lowest AIC was selected as the one best describing the data (Anderson et al., 2000).

2.3. *Relationship between fishing effort and abundance*

Fishing has been identified as the main potential threat to a river stingray in the middle and lower Paraná River (Lucifora et al., 2016). We evaluated the relationship between the abundance of river stingrays (including *P. motoro*) and the proportion of stingrays with healed cut tails. A higher proportion of tailless stingrays will be found in areas with a high fishing pressure on stingrays as compared to areas with low fishing pressure on them (Rincon, 2006). Our rationale was that no relationship between abundance estimates and proportion of stingrays with cut tails is expected, if abundance trends are not related to fishing pressure. Therefore, we calculated the proportion of stingrays with cut tails for six areas along the middle and lower Paraná River. For the same areas, relative abundance was estimated using the best model for the whole genus *Potamotrygon*. We used this model because the calculation of the proportion of tailless stingrays included specimens of all species (including *P. motoro*) to maximise sample size. Afterwards, we estimated the relationship between relative abundance (dependent variable) and proportion of tailless stingrays (independent variable). This model had a Gamma error distribution and a log link. The Gamma distribution was used because variance was not constant and the dependent variable was continuous and could take only positive values. This analysis was repeated twice. One time with the two northernmost areas separated, and a second time with both areas pooled, to account for a low sample size in one area.

3. Results

3.1. *Temporal trends*

Our first analysis revealed that the abundance of the genus *Potamotrygon* in the middle and lower Paraná River decreased by 15% annually between 2005 and 2016 (Fig. 2a). The best model for the whole genus included the variables year, latitude and hydrometric level. Coefficients of this model, with standard error in parentheses, were: intercept = 339.701 (82.819), $Y = -0.160$ (0.041), $L = -0.599$ (0.109), $H = -0.478$ (0.167). Abundance decreased with all three independent variables, as their negative signs indicate. The coefficient for year can be interpreted as the instantaneous population growth rate (r); this means that the abundance of *Potamotrygon* in the lower and middle Paraná River decreased at an annual rate of almost 15% between 2005 and 2016. The effect of latitude indicated that river stingrays were significantly more abundant in the northern part of the study area than in the southern part.

The abundance trend for *P. motoro*, our second analysis, was stable (Fig. 2b). The best model for this species included only latitude and hydrometric level, meaning that its abundance did not change significantly among years. Coefficients of the model were: intercept = 11.207 (4.229), $L = -0.416$ (0.133), $H = -0.619$ (0.210). The effect of latitude and hydrometric level was the same as for the previous analysis. In the third analysis, we excluded *P. motoro* to obtain an estimate of population change for the remaining species. The best model for this analysis retained the same variables and with the same signs as the one at genus level including *P. motoro*; its coefficients were: intercept = 612.470 (115.834), $Y = -0.295$ (0.057), $L = -0.720$ (0.146), $H = -0.413$ (0.225). Thereby, the decline was more marked, with an annual rate of 25% (Fig. 2c).

3.2. *Relationship between fishing effort and abundance*

The analysis of the relationship between abundance estimates and proportion of stingrays with cut tails indicated that, in six areas along the middle and lower Paraná River, stingray abundance was negatively related to the proportion of individuals with no tails (Fig. 3). This implies that areas with high fishing pressure on river stingrays have the lowest abundances. When the analysis was run pooling the two northernmost areas together, results were almost identical (Fig. 3).

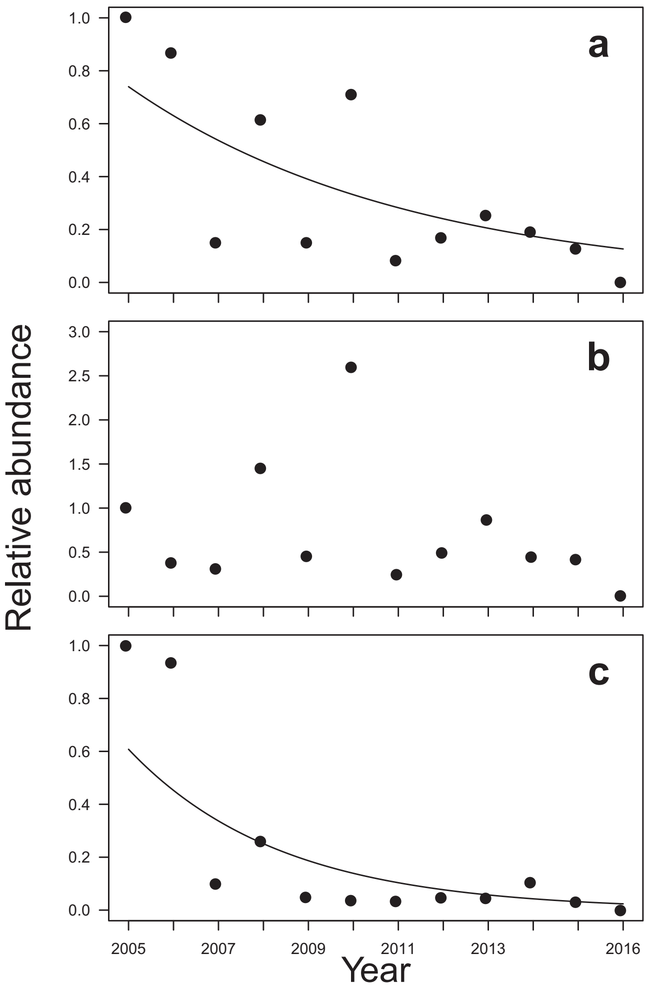

Fig. 2. Temporal trends in relative abundance of river stingrays, *Potamotrygon* spp., in the middle and lower Paraná River. The trend for all combined species of *Potamotrygon* is shown in (a), for *P. motoro* is shown in (b), and for all combined species of *Potamotrygon* excluding *P. motoro* is shown in (c). In all panels, dots are estimates for individual years from a generalized linear model with year, latitude and hydrometric level, as independent variables. In (a) and (c) the line is the estimated trend from the same models.

4. Discussion

Our analysis provides the first quantitative evidence of a population decline for any obligate freshwater elasmobranch. Previously, all evidence of population declines in elasmobranchs was from marine or euryhaline species (Baum et al., 2003; Ferretti et al., 2008, 2016; Field et al., 2009; Dulvy et al., 2016). We show that obligate freshwater elasmobranchs are susceptible to anthropogenic threats, such as fishing, as has long been hypothesised (Compagno and Cook, 1995; Rosa et al., 2010; Lucifora et al., 2015).

Fishing activities in the middle and lower Paraná River are heterogeneously distributed, which explains the latitudinal cline in both, abundance and fishing pressure on stingrays. The northern half of the middle Paraná, from the confluence with the Paraguay River to Reconquista (Fig. 1), is characterized by having artisanal fisheries targeting mainly sorubim catfishes (*Pseudoplatystoma* spp.) and stringent measures to control fishing effort are in place to ensure the presence of large fishes for recreational fisheries, which are important as a source of touristic revenue (Quirós et al., 2007; del Barco, 2008). The main fishing grounds of this area are located in the river's main channel (Vargas et al., 2004; Quirós et al., 2007; Vargas, 2016). On the other hand, in the southern half of the middle Paraná and in the lower Paraná, fishing effort is much higher than in the north and the main target fish species is a detritivorous characoid, the sábalo (*Prochilodus lineatus*) (Quirós et al., 2007; del Barco, 2008; Baigún et al., 2013). For this reason, most fishing effort is on lakes and channels of the floodplain, rather than in the main channel of the river (Baigún et al., 2013). In addition, mesh size is larger in the north area of the middle Paraná than in the southern area. Mesh size is mostly between 20 and 27 cm and as low as 16 cm in the north, as compared to 12 cm in the south (Baigún et al., 2013; Vargas, 2016). These latitudinal differences in fishing effort, fishing grounds, and mesh size can explain the contrasting latitudinal pattern of stingray abundance and proportion of individuals with cut tails. Current evidence, albeit limited (Rosa et al., 2010), suggests that stingrays are more common in shallow areas, such as floodplain lakes and secondary channels, than in main channels of big rivers (Garrone Neto and Uieda, 2012). In addition, gillnets with a large mesh size (20–27 cm) would result in low stingray catches. In fact, no stingrays have been recorded in commercial catches from the north area (Vargas et al., 2004; Vargas, 2016). These differences indicate that the development of fisheries for more valuable bony fishes with low bycatch of obligate freshwater elasmobranchs is possible, by adjusting fishing grounds and gear.

It is generally thought that habitat degradation and fishing have a more balanced weight as threats to freshwater elasmobranchs (Compagno and Cook, 1995; Field et al., 2009; Rosa et al., 2010; Dulvy et al., 2014; Lucifora et al., 2015). The relative importance of habitat degradation and fishing as threats may differ regionally. A recent assessment of potential threats to *P. brachyura* shows that the main threat to this species in the Paraná-Paraguay riverine axis would be fishing rather than habitat modification, since its geographic distribution significantly overlaps with areas of high fishing pressure (Lucifora et al., 2016). This is explained by the relatively good conservation status of the aquatic habitat of the middle Paraná-Paraguay riverine axis, which is free from major infrastructure developments (*e.g.* dams) and pollution is limited to few urban areas (Quirós et al., 2007). The evidence presented here confirms that fishing, rather than habitat modification or pollution, can be the prevalent threat to obligate freshwater elasmobranchs, as is the case for many freshwater fishes worldwide (Allan et al., 2005). The situation in the Paraná River can be similar to other areas that sustain obligate freshwater elasmobranch populations where habitat modification is considered to be low, but where fishing pressure is high, such as some areas of the Amazon (Junk et al., 2007) and Orinoco (Rodríguez et al., 2007) basins.

While we could not estimate species-specific population trends for most species, the precautionary principle indicates that some species should be closely monitored. For example, *P. brachyura* achieves a very large size, a trait that is usually correlated with low biological productivity (Dulvy et al., 2014). In recent years, this species became actively hunted by both recreational and commercial fishermen (Lucifora et al., 2016), which suggests that it might be an important contributor to the genus-level observed decline. The very rare *P. schuhmacheri*, which is endemic to the middle Paraná and Paraguay rivers (Rosa et al., 2010) should also be considered a species of global conservation concern.

The stable abundance trend of *P. motoro* indicates that some species of obligate freshwater elasmobranchs would be productive enough as to support fishing levels that make other species to decline. In the lower Amazon basin, exploited populations of *P. motoro* are also stable (de Araújo et al., 2004). The ability of *P. motoro* to withstand levels of fishing that make other species to decline may be explained, at least partially, by a conserved "fast" life history pattern among different populations of *P. motoro*. Life history is fragmentarily known for most obligate freshwater elasmobranchs yet as to assess general interspecific patterns in river stingray productivity. However, some species are known to reach sexual maturity as early as 2 years, such as *P. wallacei* (de Carvalho et al., 2016), which suggests that species with potential for sustainable exploitation may occur beyond the Paraná River.

Our analysis of fishing pressure as indicated by tail mutilation has

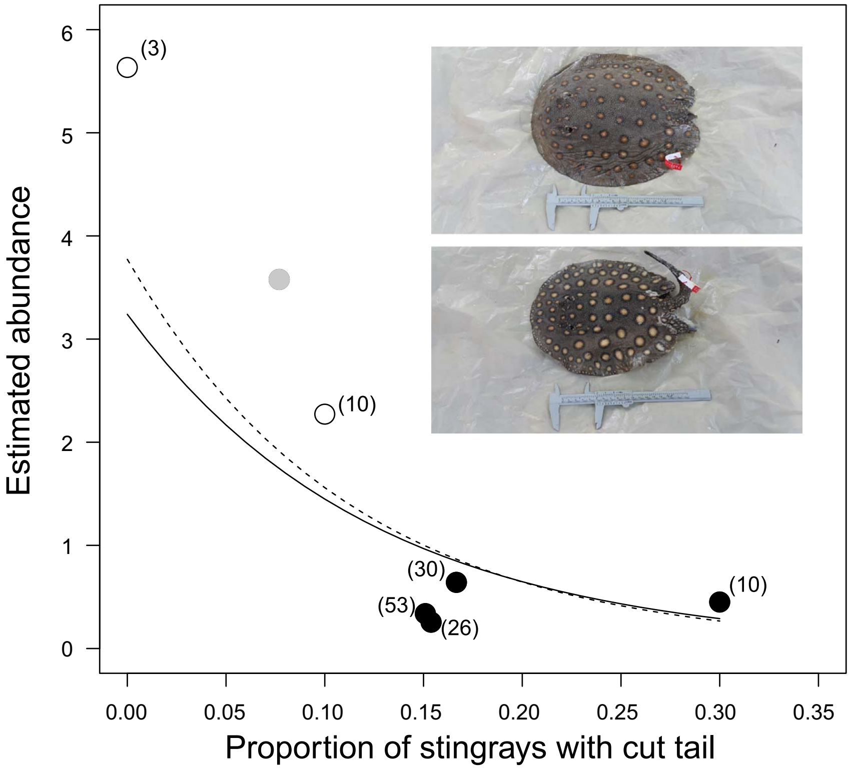

Fig. 3. Relationship between the proportion of river stingrays, *Potamotrygon* spp., caught with cut and healed tails for different areas along the middle and lower Paraná River. Empty circles represent the two northernmost areas, the grey dot represents these two northernmost areas pooled together. The solid line is the relationship estimated using data represented by black and grey dots. The dashed line is the relationship estimated using data represented by black dots and empty circles. Numbers are the number of stingrays examined in each area. The pictures show individuals of *P. motoro* with cut and healed tail (above) and with intact tail (below). In both pictures, caliper aperture is 5 cm.

some implicit assumptions that are reasonably met. First, that stingrays do not perform long-distance migration. There are few studies on river stingray movements but they indicate a high site-fidelity. Rincon (2006) used tail cutting as a mark to identify individuals of *Potamotrygon orbignyi* in a reach of the Paranã River of the Tocantins basin (not to be confused with the Paraná River of this study). The vast majority, 145 out of 147 recaptured individuals, stayed within 2 km of the release site, whereas the remaining two individuals were found just 3 and 4.5 km from the release site (Rincon, 2006). A conventional mark-and-recapture study conducted in the Paraná River also found high site fidelity. All of the recaptures (8 out of 182 marked individuals) of *Potamotrygon falkneri* and *P. cf. motoro* were made within 8 km of the release site, after as long as 12 months of initial release (Garrone Neto et al., 2014). Therefore it is reasonable to assume that river stingrays do not move extensively, at least the small and medium-sized species.

A second assumption of our analysis is that fishermen practice tail mutilation throughout the study area. Although there are no quantifications of the incidence of this practice, it is well known that tail mutilation is widespread along the Paraná River and in most other South American river basins where river stingrays occur (Castex, 1963; Rincon, 2006; Duncan et al., 2010; Garrone Neto, 2010; Oddone et al., 2012; Gama and Rosa, 2013; Rincon et al., 2013). In addition, Rincon (2006) has shown that the abundance of tailless river stingrays decreases with distance from fishing villages, which indicates a direct relationship between stingray tail mutilation and fishing effort.

Historically, river stingrays lived at high densities in the middle Paraná River. In 1774, in a description of the fishes of the middle Paraná River, Thomas Falkner wrote: “The rayas, rays, or skate, are so very plentiful in the Parana, that the shallow sandbanks are entirely covered with them” (Falkner, 1774). This is still the case in places where fishing pressure is low and where the habitat is still in fairly good condition, such as in the upper Corriente River of the Iberá marshlands, Argentina (Supplementary movie). Our results show that such high abundances can decline within a decade, at least for some species. Still much needs to be done to identify the species that are most impacted and to identify the main natural drivers of variation in abundance of river stingrays in particular, and freshwater elasmobranchs in general.

An additional supplementary movie is provided.

Acknowledgements

We thank Silvia C. Zaninovich for permission to use the Supplementary movie, Boris Worm for discussion on an early version of this paper, and two anonymous reviewers for helpful comments. This work has been funded by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) [grant PIP 11220120100054]; and by Agencia Nacional de Promoción Científica y Tecnológica [grant PICT 2014-0660], both from Argentina.

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