Geographic distribution of the short-tailed river stingray (*Potamotrygon brachyura*): assessing habitat loss and fishing as threats to the world's largest obligate freshwater elasmobranch

Luis O. Lucifora[A,H], *Santiago A. Barbini*[B], *Sabina Llamazares Vegh*[C],
Pablo A. Scarabotti[D], *Facundo Vargas*[E], *Agustín Solari*[A,F],
Ezequiel Mabragaña[G] *and Juan M. Díaz de Astarloa*[G]

[A]Instituto de Biología Subtropical – Iguazú, Consejo Nacional de Investigaciones Científicas y
  Técnicas (CONICET), Universidad Nacional de Misiones, Casilla de Correo 9, Puerto Iguazú,
  Misiones, N3370AVQ, Argentina.
[B]Laboratorio de Ictiología, Instituto de Investigaciones Marinas y Costeras, CONICET,
  Universidad Nacional de Mar del Plata (UNMdP), Funes 3350, Mar del Plata, Buenos Aires,
  B7602YAL, Argentina.
[C]Dirección de Pesca Continental, Dirección Nacional de Planificación Pesquera, Subsecretaría
  de Pesca y Acuicultura, Ministerio de Agricultura, Ganadería y Pesca, Alférez Pareja 125,
  Ciudad Autónoma de Buenos Aires, C1107, Argentina.
[D]Instituto Nacional de Limnología, CONICET, Universidad Nacional del Litoral,
  Ciudad Universitaria, Paraje El Pozo, Santa Fe, Santa Fe, S3001XAI, Argentina.
[E]Departamento Fauna y Pesca, Dirección de Fauna y Áreas Naturales Protegidas,
  Remedios de Escalada 46, Resistencia, Chaco, H3500BPB, Argentina.
[F]Centro de Investigaciones del Bosque Atlántico, Bertoni 85, Puerto Iguazú, Misiones,
  N3370BFA, Argentina.
[G]Laboratorio de Biotaxonomía Morfológica y Molecular de Peces, Instituto de Investigaciones
  Marinas y Costeras, CONICET, UNMdP, Funes 3350, Mar del Plata, Buenos Aires,
  B7602YAL, Argentina.
[H]Corresponding author. Email: luis.lucifora@conicet.gov.ar

Abstract. Freshwater elasmobranchs are threatened but little is known about them. *Potamotrygon brachyura* is the world's largest obligate freshwater elasmobranch. This makes it popular among fishermen and suggests a susceptibility to anthropogenic threats. We collected records of *P. brachyura* ($n = 70$) from media, fishermen and scientific sampling, to estimate its global geographic distribution (using both generalised additive and MaxLike models). Then, we estimated the species' exposure to habitat modification and fishing pressure, by applying multinomial ordinal models with threat levels as response and the presence or absence of *P. brachyura* as an independent variable. Distance to coast, depth, water temperature range, salinity range and mean water temperature were the main determinants of the distribution in the Río de la Plata. This resulted in a narrow coastal distribution. In the Uruguay and Paraná River basins, the probability of occurrence was positively associated with flow accumulation, percentage of open water and submerged vegetation, and lowland ecoregions, and negatively to wetness index and altitude. This limited the distribution to large lowland rivers. Approximately 41% of the range of *P. brachyura* in the Río de la Plata was subject to high habitat modification. In the Uruguay and Paraná River basins, this percentage reached 7%; however, the overlap with high fishing pressure was 59%. For conservation purposes, *P. brachyura* may function as an umbrella species.

Additional keywords: Chondrichthyes, Pantanal, Paraná River, Río de la Plata basin, South America, species distribution modelling, wetlands.

Introduction

Freshwater environments contain a disproportionate amount of biodiversity and are among the most threatened ecosystems on earth (Dudgeon *et al.* 2006). Despite being among the less extensive environments, freshwater ecosystems harbour a great number of species. Fishes, for example, are proportionally much more diverse in fresh water than in marine ecosystems: 40–45% of all fish species inhabit exclusively freshwater habitats that represent less than 1% of all aquatic habitat on earth (Lévêque *et al.* 2008). Owing to its small size (as compared to marine ecosystems) and to its primary importance to humanity, freshwater ecosystems are among the most modified and threatened (Dudgeon *et al.* 2006). Habitat modification, pollution and overexploitation are the main threats affecting freshwater biodiversity (Allan *et al.* 2005; Dudgeon *et al.* 2006; Humphries and Winemiller 2009; Collen *et al.* 2014). As a result, 56–71% of the world's natural inland (freshwater) wetlands have been lost, with 69–75% lost during the 20th century, despite conservation efforts, such as the Ramsar Convention (Davidson 2014), and freshwater species are at a higher risk of extinction than terrestrial ones (Collen *et al.* 2014). This is of particular concern for freshwater taxa that are unique from an ecological (e.g. keystone species), biogeographic (e.g. endemic species), or evolutionary (e.g. species representing unique clades) point of view.

The class Chondrichthyes (subclasses Elasmobranchii (sharks, skates and rays) and Holocephali (chimaeras)) comprises ~1200 species, predominantly marine. However, a significant minority of species (~14%) are able to survive in estuaries or fresh water (Compagno 1990; Dulvy *et al.* 2014). Furthermore, some species are fully adapted to fresh water and do not survive in marine waters; these are known as obligate freshwater elasmobranchs (Compagno and Cook 1995; Compagno 2002). These species, belonging to the order Myliobatiformes (stingrays and allies), inhabit tropical and subtropical water bodies of South America, west Africa, and south-east Asia, although the greatest number of species (28 of 34) occur in South America (Compagno 2002). South American freshwater stingrays are unique because they represent an evolutionarily distinct clade of chondrichthyans, the family Potamotrygonidae, with physiological and ecological adaptations to life in tropical and subtropical freshwater environments (Rosa *et al.* 2010). Physiological adaptations include the reduction of the salt-excreting rectal gland and the loss of urea retention in the blood. Ecological adaptations include a match of reproductive cycles to hydrographic regimes and surface swimming when oxygen concentration is low (Rosa *et al.* 2010). In general, freshwater elasmobranchs are less well known than marine ones and most of the basic information needed to assess their conservation status, such as geographic distribution, is lacking (Dulvy *et al.* 2014).

Although overfishing is the main threat for an overwhelming majority (~96%) of marine elasmobranchs (Ferretti *et al.* 2010), obligate freshwater elasmobranchs could also be threatened by other threats (Compagno and Cook 1995; Compagno 2002; Dulvy *et al.* 2014). As compared to their marine relatives, obligate freshwater elasmobranchs live in smaller, more variable and patchier environments (Compagno and Cook 1995; Dulvy *et al.* 2014). This makes them vulnerable to different forms of habitat loss, such as physical habitat alteration (e.g. dams and reservoirs, channelisation, siltation, deforestation) and different forms of pollution (e.g. point source, mining, agricultural pollution) (Compagno and Cook 1995). In fact, for the only three species of *Potamotrygon* that could be evaluated by the International Union for Conservation of Nature (IUCN) beyond the Data Deficient category, a combination of overfishing and habitat loss are recognised as realised or potential threats (Rincon 2004; Araújo *et al.* 2009; Charvet-Almeida and Almeida 2009).

The short-tailed river stingray (*Potamotrygon brachyura*), endemic to the Río de la Plata basin, is one of the most conspicuous obligate freshwater elasmobranchs. Weighing up to 208 kg, it is the largest obligate freshwater fish in South America, rivalled only by the teleostean pirarucus (*Arapaima* spp.), and the piraíba giant catfish (*Brachyplatystoma filamentosum*), which may both attain 200 kg (Allan *et al.* 2005). It is also the largest obligate freshwater elasmobranch in the world, as the giant freshwater whipray (*Himantura polylepis*) is now known to occur in marine waters in addition to fresh water (Last *et al.* 2010). Because of its large size, *P. brachyura* is hunted by big-game fishermen, and its captures are usually reported by local and national newspapers, fishing magazines and newscasts.

Despite its popularity among regional fishermen, the ecology and conservation status of *P. brachyura* remain completely unknown. Although there are a few studies on the ecology of other freshwater stingrays from the Río de la Plata basin (e.g. Martínez Achenbach and Valentinis de Martínez Achenbach 1976; Garrone-Neto 2010; Garrone-Neto and Uieda 2012), no scientific studies focussing on the biology and ecology of *P. brachyura* have been published so far. Not surprisingly, the conservation status of *P. brachyura* is unknown because it could not be evaluated by any of the analyses of conservation status in which the species was included, even though they were based on different methodological approaches (i.e. Charvet-Almeida *et al.* 2009; Chebez *et al.* 2009; Peteán 2009; Baigún *et al.* 2012). Despite this lack of information, *P. brachyura* is thought to be affected primarily by habitat modification (Charvet-Almeida *et al.* 2009) and it has been declared a priority species for conservation in Uruguay (Loureiro *et al.* 2013).

In this paper, we took advantage of the conspicuousness of *P. brachyura* and its popularity among fishermen to gather data on the occurrence of this species throughout the Río de la Plata basin. In addition to specimens from scientific collections and sampling, we looked for confirmable records of *P. brachyura* provided by fishermen and recreational fishing magazines. Our objectives were (1) to estimate the geographic distribution of *P. brachyura* and (2) to assess the threat of habitat loss and fishing pressure to *P. brachyura* by quantifying the overlap of its geographic range with different levels of these threats.

Material and methods

Study area

Covering over $3 \times 10^6 \, km^2$, the Río de la Plata basin is the second largest drainage system in South America (Dunne and Mertes 2007) (Fig. 1), and home to a rich biodiversity. This basin contains some of the world's largest tropical and subtropical rivers (e.g. Paraná, Paraguay, Uruguay) and the planet's
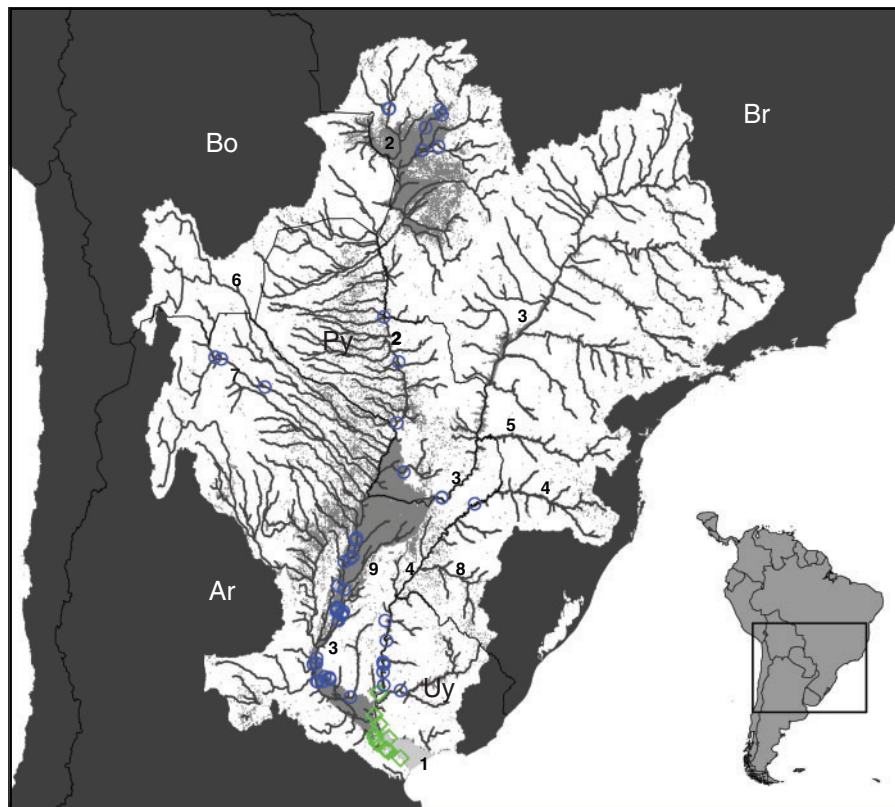
Fig. 1. Occurrence records of the short-tailed river stingray (*Potamotrygon brachyura*) in rivers (grey lines) and wetlands (dark grey areas) of the Río de la Plata basin (white area). The inner, freshwater zone of the Río de la Plata is shown in light grey. Records for the Río de la Plata and lower Uruguay rivers are shown as diamonds; records for the Uruguay and Paraná (including the Paraguay) river basins are shown as circles. International boundaries are shown as black lines. Countries: Ar, Argentina; Bo, Bolivia; Br, Brazil; Py, Paraguay; Uy, Uruguay. Rivers: 1, Río de la Plata; 2, Paraguay; 3, Paraná; 4, Uruguay; 5, Iguazú; 6, Pilcomayo; 7, Bermejo; 8, Ibicuí; 9, Corrientes. Map projection is Mollweide equal area. The inset shows the location of the depicted area in South America.

most extensive riverine wetland corridor (Peteán 2009), including the Pantanal and middle and lower Paraná river floodplain. The environments of the Río de la Plata basin are ecologically complex, with great spatial and temporal heterogeneity (Agostinho and Zalewski 1996; Menni 2004; Paira and Drago 2007; Aceñolaza *et al.* 2008; Scarabotti *et al.* 2011). This heterogeneity arises from the variety of climates (from tropical in the north to warm temperate in the southern extreme, with a humid-to-arid gradient from east to west) and topographic features (the Andes Mountain Range in the west, the Chaco and Pampas plains in the centre and south, the Brazilian Shield in the north and the Serra do Mar highlands in the east) that characterise the basin (Quirós 2004).

Data sources

Data on occurrences of *P. brachyura* throughout the Río de la Plata basin were obtained from different sources, such as scientific reports and publications, online repositories (Global Biodiversity Information Facility, GBIF), reports of fishermen's catches and our own sampling. For all records we either examined the actual specimens or images of them to check

species identification based on Rosa (1985). We cannot make public images of specimens from records whose source is not our own sampling, but they are available from the authors upon request.

Sampling was conducted in multiple locations along the middle Paraná River, as part of a project aiming to evaluate the biodiversity and population status of fish species of the lower Paraguay and middle Paraná rivers, conducted by the Argentinean *Dirección de Pesca Continental* jointly with the provinces of Entre Ríos, Santa Fe, Corrientes and Chaco. This sampling was conducted four times per year (once per season) using gill-nets of multiple mesh size in each location, to sample the widest possible fish size range. All freshwater stingrays that were caught were photographed, preserved and deposited at the ichthyological collection of the Instituto de Biología Subtropical – Iguazú.

Geographic range estimation

We used occurrence data to estimate the geographic range of *P. brachyura* through species distribution modelling. The modelling approach differed according to data availability.

For the Río de la Plata and lower Uruguay River (RdlP), we used two different methodological approaches. The first, preferred, approach was a generalised additive model (GAM) with a binomial distribution run on actual presences and absences of *P. brachyura* and using environmental correlates as predictors. For this region, we had absence data available from FREPLATA (2004). These absences consisted of trawl stations where *P. brachyura* was not caught. Presence data for RdlP included trawl stations with positive catches of *P. brachyura*, plus other records. The second approach was a presence–background technique, called MaxLike (Royle *et al.* 2012), that uses presence data plus environmental predictors to estimate the probability of occurrence of a species, and is being increasingly used in species distribution modelling (e.g. Sarre *et al.* 2013; Fitzpatrick *et al.* 2013; Ferrer-Paris *et al.* 2014; Sánchez-Mercado *et al.* 2014).

For the rest of the Río de la Plata basin, i.e. the Uruguay and Paraná (including the Paraguay) river basins (UP), we were able to use MaxLike because we only had presence data. For this region, we built 10 different datasets because there was a tendency in the data to over-represent the southern part of the basin. Then, we excluded data from aggregations in the southern part of the UP and randomly assigned one point of each aggregation to one dataset, following Legault *et al.* (2013). In this way, we obtained a more balanced dataset to run the MaxLike models. We first selected the best model using one of the 10 datasets selected at random. Then, we reran the best model for each of the 10 datasets. The mean of the ten runs of the best model was our final estimation of the geographic range of *P. brachyura* in the UP. In MaxLike models of both regions, we included a quadratic term for each predictor in order to account for potential non-linear effects (Royle *et al.* 2012). For both modelling approaches, the best model was selected by minimising the Akaike Information Criterion (AIC) (Anderson *et al.* 2000).

The set of predictors used in the modelling also differed between regions. For the RdlP, we used depth, mean surface temperature, mean surface salinity, annual range in surface salinity, annual range in surface temperature, surface temperature of the warmest month, and distance to shore. These environmental predictors were taken from the database built by Sbrocco and Barber (2013). Because a database of these hydrographic predictors does not exist for the whole Río de la Plata basin, we used a mixture of climatic, topographic, hydrographic and biogeographic predictors for the UP. These predictors were isothermality (i.e. mean diurnal temperature range ÷ annual temperature range), altitude (Hijmans *et al.* 2005), flow accumulation (http://www.worldwildlife.org/pages/hydrosheds, accessed 14 February 2014; a measurement of the upstream catchment area and stream order), percentage of flooded vegetation, percentage of open water (Tuanmu and Jetz, 2014), topographic wetness index (calculated by ourselves from altitude and flow accumulation), distance to urban centres with human density higher than 500 inhabitants km^{-2} (to account for a potential bias of having more records closer to places with more fishermen: de Resende 2003), and an ecoregion factor. The ecoregions of the Río de la Plata basin are Paraguay, Chaco, Upper Paraná, Lower Paraná, Iguazú, Upper Uruguay and Lower Uruguay, as defined by Abell *et al.* (2008). However,

the Lower Paraná ecoregion is too vast and includes sub-basins with marked environmental and biogeographic differences, which challenges the view of the Lower Paraná as a single ecoregion (Menni 2004). For the purpose of this study, the main biogeographic difference is the ichthyofaunistic relationship of the western part of the Lower Paraná ecoregion with the more southern Pampean ecoregion (not included in this study), as indicated by López *et al.* (2008). Then, we identified the western part of the Lower Paraná ecoregion as a different ecoregion related to the Pampean biogeographic unit of López *et al.* (2008). The Upper Paraná, Iguazú, Upper Uruguay and Pampean ecoregions are all devoid of any recent or historical record of *P. brachyura* (e.g. Menni 2004; Garrone-Neto *et al.* 2007; López *et al.* 2008; Júlio Júnior *et al.* 2009). Then, the ecoregion factor was a categorical variable defining the Paraguay, Chaco, Lower Paraná and Lower Uruguay as ecoregions with presence of *P. brachyura* and the remaining ones as ecoregions with absence of *P. brachyura*. We did not include together in the same model predictors with a correlation coefficient (*r*) higher than 0.5.

All data manipulation and modelling were conducted in R ver. 3.1.1 (R Core Team 2014), using the packages MASS (Venables and Ripley 2002), raster (Hijmans 2014), mgcv (Wood 2006) and maxlike (Royle *et al.* 2012).

Habitat loss and fishing pressure

We estimated the degree of exposure of *P. brachyura* to habitat loss by estimating the overlap of the estimated geographic range to different categories of habitat modification, ranging from near pristine to highly degraded conditions.

First, from the maps of probability of occurrence, we obtained a binary (i.e. presence–absence) map by applying a threshold of occurrence to the probability of occurrence. The threshold applied was the one that maximised the sum of sensitivity and specificity (Liu *et al.* 2013).

Second, we categorised all the aquatic habitat of the Río de la Plata basin in an ordinal scale of habitat modification going from pristine to highly modified. Again, the categorisation necessarily differed between the two regions considered because of differences in the data. For the RdlP, we used the scale and geographic coverage of biodiversity threats estimated by Brazeiro *et al.* (2003). This scale identifies four ordinal levels of threats in the RdlP based on four kinds of stressors: biological invasions (by both molluscs and fish), biological contamination (e.g. harmful algal blooms), pollution (chemicals, heavy metals, bottom solid debris, coastal point sources of pollution) and benthic habitat alteration (dredging, bottom trawl damage) (Brazeiro *et al.* 2003). For the UP, we used six ordinal categories of the Human Influence Index from Wildlife Conservation Society and Center for International Earth Science Information Network, Columbia University (2005). The Human Influence Index takes into account the effect of stressors such as human population pressure, human land use and infrastructure (including dams and reservoirs), and human access (including river and lake navigation).

Finally, for each region, we overlapped the geographic distribution of *P. brachyura* obtained from the binary map with the map of habitat modification. In this way, we obtained an ordinal distribution of habitat modification categories for

aquatic habitats where *P. brachyura* is either present or absent. We measured the overlap between the geographic distribution of *P. brachyura* and the different categories of habitat modification as the probability of any given pixel of the geographic range of *P. brachyura* to fall in any of the habitat modification categories. This was accomplished by fitting a multinomial ordinal model, where habitat modification was the response variable, and presence or absence of *P. brachyura* was the independent variable (Faraway 2006).

Data on fishing pressure in the UP were taken from the database of human stressors on freshwater biodiversity built by Vörösmarty *et al.* (2010). This database includes data on the global spatial distribution of relative fishing pressure in freshwater environments, with a spatial resolution of 0.5° longitude by latitude. We bilinearly interpolated these data for the Río de la Plata basin environments in order to have them at the same resolution as the rest of the analyses. Then, we measured the overlap of the geographic distribution of *P. brachyura* with five different ordinal categories of fishing pressure (from low to high), in an analogous way as we did for habitat modification.

For these analyses we used the packages MASS, raster and PresenceAbsence (Freeman and Moisen 2008) in R, ver. 3.1.1.

Results

Geographic range

We were able to obtain 74 putative records of *P. brachyura* in the Río de la Plata basin. For most of them (70; 12 from the RdlP and 58 from the UP) (Table 1), the identity of the species involved could be positively determined as *P. brachyura*, from either direct examination of the specimens, or photographs, videos or drawings of the actual specimens recorded. One record of a specimen from the Paraguay River, near Asunción (Paraguay), housed in the Australian Museum and obtained through GBIF, labelled as *P. brachyura* was found to represent a different species upon examination of photographs; therefore it was excluded from our analyses. A specimen unequivocally assignable to *P. brachyura* was caught in Formosa (Argentina), but no further details of the location (water course or body) were available and so was not included in our analyses. Another record from the Ibicuí River (Rio Grande do Sul, Brazil) assigned to *P. brachyura* (Behr 2005) was not included because no photograph or specimen were available. Finally, a putative record of a large stingray from the Corrientes River (Corrientes, Argentina) was not included because the available photographs showed only a dressed specimen with no visible diagnostic characters, other than its large size.

Positive records were distributed throughout the Río de la Plata basin. However, they were conspicuously absent from the upper Paraná River basin, the Iguazú River basin and the upper Uruguay River basin (Fig. 1). Records tended to be concentrated in the southern half of the basin, particularly in the lower Paraná and Uruguay rivers.

Records of *P. brachyura* in the RdlP were always close to shore, whereas regions of the RdlP far away from shore were characterised by the absence of *P. brachyura* (Fig. 2a). Both, MaxLike and GAM models produced a very similar geographic distribution of *P. brachyura* in the RdlP (Fig. 2b, c). The best MaxLike model predicted the highest probability of occurrence

of *P. brachyura* close to the shores of the RdlP (Fig. 2b). This model (parameters given within parentheses) included distance to shore (−274.8), depth (34.2) and mean surface temperature (40.9) as environmental predictors (Table 2) plus an intercept (−383.5). There were two GAM models with indistinguishable fit (Table 2). These models each included (1) distance to shore, depth, mean surface salinity, and range of surface temperature and (2) distance to shore, depth, range of surface salinity and range of surface temperature (Table 2). The average of the two best GAM models produced a pattern with the highest probability of occurrence close to shore, but it included the whole lower Uruguay River as an area of high probability of occurrence for *P. brachyura* (Fig. 2c).

The best MaxLike model for the UP included flow accumulation, altitude, topographic wetness index, percentage of flooded vegetation, percentage of open water and ecoregion (Table 3). Parameters of the best model (with standard deviation) were: intercept = −102.24 (13.12), flow accumulation = 18.37 (0.30), altitude = −13.16 (0.53), topographic wetness index = −2.33 (0.05), percentage of flooded vegetation = 0.46 (0.02), percentage of open water = 4.74 (0.06), ecoregion = 89.83 (13.12). This model predicted a high probability of occurrence of *P. brachyura* only along the largest rivers of the UP, and their associated floodplains, such as the Paraguay and the middle and lower Paraná rivers, and wetlands, such as the Pantanal (Fig. 3). Other major rivers of the UP were also identified as having available habitat for *P. brachyura*, such as the Bermejo, Pilcomayo, Monte Lindo, Timane, Corixa Grande, Cuiabá, Taquarí, Tebicuary, lower Salado, Gualeguay, middle Uruguay and Negro rivers (Fig. 3). Interestingly, rivers with unconfirmed records of *P. brachyura* (i.e. records not included in the models) were also predicted to have high probability of occurrence for the species, such as the Ibicuí and Corrientes rivers (Fig. 3).

Applying a threshold that maximises the sum of sensitivity and specificity (0.159) to the best model for the UP produced a binary map (Fig. 4) that included all the main rivers with high probability, but also the main wetlands of the UP, such as the Pantanal, Iberá, Riachuelo, wetlands of southern Paraguay and the Bajos Submeridionales (Fig. 4). Remarkably, although all the main rivers of ecoregions where *P. brachyura* was not recorded were not identified as potential habitat for the species, the upper Paraná River did include some potential habitat for *P. brachyura* (Fig. 4).

Habitat loss threat

The application of a threshold that maximises the sum of sensitivity and specificity (0.495) to the best GAM model of the RdlP showed that most of the geographic range of *P. brachyura* in the RdlP fell in the lowest and in the second highest threat category (Fig. 2d). The probability of any given pixel of the geographic range of *P. brachyura* in the RdlP falling in any of the threat categories as estimated by a multinomial ordinal model, from lowest to highest, were: 0.4836, 0.1040, 0.3347 and 0.0777. This means that ~41% of the geographic range of *P. brachyura* in the RdlP is subject to high habitat modification, whereas the remainder of the species' range lies in slightly modified habitat.

Table 1.   Occurrence records of the short-tailed river stingray (*Potamotrygon brachyura*) used in the estimation of its geographic distribution in the Río de la Plata basin

A record (number 21) of the largest known specimen, caught in 2007, reportedly weighing 208 kg, is marked with an asterisk

Record number	Longitude (W)	Latitude (S)	Country	River	Reference
1	57.753	16.145	Brazil	Paraguay	Unpublished
2	57.770	16.161	Brazil	Paraguay	Unpublished
3	55.964	16.184	Brazil	Cuiabá	Unpublished
4	55.893	16.333	Brazil	Mutum	Unpublished
5	56.466	16.689	Brazil	Cuiabá	Rosa (1985)
6	56.014	17.228	Brazil	Piquirí	Unpublished
7	56.585	17.330	Brazil	Piquirí	Unpublished
8	56.595	17.332	Brazil	Piquirí	Unpublished
9	57.993	22.090	Brazil	Confluence Apa and Paraguay	Unpublished
10	64.130	23.251	Argentina	Bermejo	Monasterio de Gonzo (2003)
11	63.903	23.303	Argentina	Bermejo	Unpublished
12	57.460	23.391	Paraguay	Paraguay	Unpublished
13	62.349	24.115	Argentina	Bermejo	Monasterio de Gonzo (2003)
14	57.542	25.153	Paraguay	Paraguay	Unpublished
15	57.297	26.583	Paraguay	Tebicuary	Unpublished
16	55.891	27.318	Paraguay	Paraná	Unpublished
17	55.885	27.327	Paraguay	Paraná	Unpublished
18	55.895	27.330	Paraguay	Paraná	Unpublished
19	54.677	27.507	Brazil	Uruguay	Unpublished
20	59.082	28.507	Paraguay	Paraná	Unpublished
21*	59.113	28.576	Argentina	Paraná	Unpublished
22	59.223	29.048	Argentina	Paraná	Unpublished
23	59.341	29.119	Argentina	Paraná	Unpublished
24	59.555	29.207	Argentina	Paraná	Unpublished
25	59.809	29.910	Argentina	Paraná	Unpublished
26	59.566	30.014	Argentina	Paraná	Unpublished
27	59.841	30.546	Argentina	Paraná	Unpublished
28	59.840	30.582	Argentina	Paraná	Unpublished
29	59.844	30.589	Argentina	Paraná	Unpublished
30	59.877	30.593	Argentina	Paraná	Unpublished
31	59.877	30.666	Argentina	Paraná	Unpublished
32	59.619	30.674	Argentina	Paraná	Unpublished
33	59.676	30.724	Argentina	Paraná	Unpublished
34	59.674	30.747	Argentina	Paraná	Unpublished
35	59.678	30.748	Argentina	Paraná	Unpublished
36	59.668	30.749	Argentina	Paraná	Unpublished
37	59.685	30.786	Argentina	Paraná	Unpublished
38	59.809	30.935	Argentina	Paraná	Unpublished
39	58.042	30.941	Argentina	Uruguay	Unpublished
40	58.003	31.534	Argentina	Uruguay	Unpublished
41	60.672	32.058	Argentina	Paraná	Unpublished
42	58.136	32.173	Uruguay	Uruguay	Devincenzi & Teague (1942)
43	60.687	32.201	Argentina	Paraná	Unpublished
44	58.124	32.235	Argentina	Uruguay	Oddone *et al.* (2008, 2012)
45	60.806	32.240	Argentina	Paraná	Unpublished
46	58.098	32.240	Uruguay	Uruguay	Oddone *et al.* (2008, 2012)
47	58.098	32.240	Uruguay	Uruguay	Oddone *et al.* (2008, 2012)
48	58.140	32.461	Uruguay	Uruguay	Oddone *et al.* (2008, 2012)
49	60.377	32.610	Argentina	Paraná	Sampling
50	60.377	32.610	Argentina	Paraná	Sampling
51	60.203	32.638	Argentina	Paraná	Sampling
52	60.179	32.691	Argentina	Paraná	Sampling
53	60.700	32.737	Argentina	Paraná	Unpublished
54	60.457	32.748	Argentina	Paraná	Unpublished
55	60.649	32.763	Argentina	Paraná	Unpublished
56	58.119	32.859	Uruguay	Uruguay	Oddone *et al.* (2012)
57	57.477	33.018	Uruguay	Negro	Serra *et al.* (2014)
58	59.407	33.216	Argentina	Gualeguay	Unpublished

(*Continued*)

Table 1.   (Continued)

Record number	Longitude (W)	Latitude (S)	Country	River	Reference
Río de la Plata and lower Uruguay rivers					
59	58.317	33.083	Argentina	Uruguay	Unpublished
60	58.492	33.748	Argentina	Uruguay	Unpublished
61	58.307	34.009	Uruguay	Uruguay	Unpublished
62	58.493	34.322	Argentina	Paraná (delta)	Unpublished
63	58.471	34.422	Argentina	Río de la Plata	Unpublished
64	57.948	34.426	Uruguay	Río de la Plata	Unpublished
65	58.404	34.564	Argentina	Río de la Plata	Unpublished
66	58.082	34.764	Argentina	Río de la Plata	Llompart *et al.* (2012)
67	58.008	34.781	Argentina	Río de la Plata	Unpublished
68	57.973	34.810	Argentina	Río de la Plata	Unpublished
69	57.965	34.819	Argentina	Río de la Plata	Unpublished
70	57.501	35.027	Argentina	Río de la Plata	Unpublished

Fig. 2.   Occurrence records and estimated geographic range of the short-tailed river stingray (*Potamotrygon brachyura*) and habitat modification levels in the Río de la Plata and lower Uruguay rivers (RdlP). (*a*) Presence (diamonds) and absence (circles) records of *P. brachyura* in the RdlP (grey area). (*b*) Probability of occurrence of *P. brachyura* in the RdlP as estimated by MaxLike models. (*c*) Probability of occurrence of *P. brachyura* in the RdlP as estimated by a generalised additive model (GAM). (*d*) Overlap of the geographic range of *P. brachyura* (outline close to the RdlP coastline) and habitat modification threat levels in the RdlP. The outline represents the geographic range of *P. brachyura* in the RdlP resulting from applying the threshold that maximises the sum of sensitivity and specificity to the results of the GAM. Habitat modification levels are taken from Brazeiro *et al.* (2003). In all panels, the thin line up the Río de la Plata and lower Uruguay rivers is the international boundary between Argentina and Uruguay. Map projection is Mollweide equal area.

Table 2. Summary of MaxLike and generalised additive models (GAM) used for estimating the geographic range of the short-tailed river stingray (*Potamotrygon brachyura*) in the Río de la Plata and lower Uruguay rivers

Models are ranked according to their Akaike Information Criterion (AIC) from lowest (best model) to highest (worst model). Predictors: D, depth; Di, distance to shore; Tmean, water surface temperature (mean); Trange, water surface temperature (range); Tmax, water surface temperature of the warmest month; Smean, surface salinity (mean); Srange, surface salinity (range). Predictors with a '2' indicate the inclusion of a quadratic term

Rank	Predictors	AIC
	MaxLike	
1	D, Di, Tmean	196.62
2	D, Di, Trange	197.12
3	D, Di, Smean, Trange	198.79
4	D, Di, Smean, Trange	198.83
5	D, Di, Srange, Trange	198.85
6	D, Di, Smean	203.02
7	D, Di, Srange	203.39
8	D, Di	204.06
9	D, Di, Smean, Tmax	204.94
10	D, Di, Tmax	205.12
11	D, Di, Srange, Tmax	205.35
12	D, Di, Di2, D2, Tmean, Tmean2	205.90
13	D, Di, Di2, D2	207.12
14	D, Di, Di2, D2, Trange, Trange2	207.69
15	D, Di, Di2, D2, Srange, Srange2, Trange, Trange2	208.00
16	D, Di, Di2, D2, Smean, Smean2, Trange, Trange2	208.72
17	D, Di, Di2, D2, Srange, Srange2	208.91
18	D, Di, Di2, D2, Smean, Smean2, Tmax, Tmax2	208.91
19	D, Di, Di2, D2, Smean, Smean2	208.98
20	D, Di, Di2, D2, Srange, Srange2, Tmax, Tmax2	209.01
21	D, Di, Di2, D2, Tmax, Tmax2	209.87
	GAM	
1	D, Di, Srange, Trange	13.69
2	D, Di, Smean, Trange	13.70
3	D, Di, Srange, Tmax	15.22
4	D, Di, Smean, Tmax	15.38
5	D, Di, Smean	15.65
6	D, Di, Srange	15.73
7	D, Di, Tmean	16.45
8	D, Di, Trange	17.51
9	D, Di	23.90
10	D, Di, Tmax	27.87

For the UP, the areas with the highest habitat modifications were located along the major rivers, particularly the Paraná, Uruguay, middle and lower Paraguay, and Iguazú rivers (Fig. 5). The Bermejo, Pilcomayo and upper Paraguay rivers, the Pantanal, Iberá and Bajos Submeridionales wetlands and large areas of the middle and lower Paraná river floodplain had a low score of habitat modification (Fig. 5). Consequently, the probability of any given pixel of the geographic range of *P. brachyura* in the UP falling into any of the threat categories, from lowest to highest, were: 0.0127, 0.5452, 0.3815, 0.0507, 0.0095 and 0.0004. This means that ~93% of the geographic range of *P. brachyura* in the UP falls in the lower half of the habitat modification scores, with ~55% of this range falling in the two lowest categories of habitat modification.

Fishing pressure threat

Fishing pressure tended to be high along all major rivers of the UP, with only a few areas in the Pantanal, Iberá and Bajos Submeridionales wetlands having low fishing pressure (Fig. 6). The probability of any given pixel of the geographic range of *P. brachyura* in the UP falling into any of the fishing pressure categories, from lowest to highest, were: 0.0297, 0.1242, 0.2570, 0.2874 and 0.3016. Then, almost 59% of the geographic range of *P. brachyura* in the UP is exposed to the two highest categories of fishing pressure, whereas only 15% of the species' range lies within areas in the lowest two categories of fishing pressure.

Discussion

Geographic distribution

The main predictors of the geographic distribution of *P. brachyura* indicate that it is associated with large lowland rivers, rather than with lentic water bodies (e.g. lakes and reservoirs). The large effect of ecoregion indicates that the upper parts of the sub-basins (i.e. upper Uruguay, Iguazú, Pampean, which corresponds with the upper Salado River) are not appropriate habitats for *P. brachyura*. This is in agreement with current evidence (Menni 2004; López *et al.* 2008; Gómez *et al.* 2009; Baumgartner *et al.* 2012). The upper Paraná ecoregion is an exception to this pattern as *P. brachyura* is predicted to occur there, mostly due to the large size of the Paraná River (see below). The negative effect of altitude is also expected because freshwater stingrays are known mostly from low-altitude ecosystems (Rosa *et al.* 2010). Some small species of *Potamotrygon* may increase in abundance after river impoundment (Rincon 2004; Garrone-Neto *et al.* 2014), suggesting that they may benefit from lentic habitats. In contrast, *P. brachyura* is negatively associated with these environments, as indicated by the negative relationship with the topographic wetness index, which measures water accumulation or the tendency of water to pool (Schaefer and Arroyave 2010), and positively associated with flowing waters, like those of large floodplain rivers, as indicated by its positive association with flow accumulation.

The main part of the geographic range of *P. brachyura* lies within the Paraguay–middle Paraná axis, including the Pantanal and the Paraná River floodplain. Other areas of importance are the middle and lower Uruguay River, coastal areas of the Río de la Plata, Bermejo, Tebicuary, Ibicuí, Corrientes and Gualeguay rivers. This is explained by the importance of flow accumulation as a determinant of the distribution of *P. brachyura* in the UP. Interestingly, some of these areas, like the Corrientes and Ibicuí rivers, have putative records of *P. brachyura* (Behr 2005). Owing to the unconfirmed nature of these records, they were not included in our models. However, our final model still identified those areas as suitable habitat for *P. brachyura*, which indicates that they may be valid. Particularly important, because of the extension of continuous wetland as habitat for *P. brachyura,* is the Paraguay–middle Paraná riverine axis.

Areas for which there are no records but which are predicted as potential habitat of *P. brachyura* include the Pilcomayo and lower Salado rivers and the Iberá and Bajos Submeridionales wetlands. These areas require further sampling to confirm the presence of *P. brachyura*. The Pilcomayo is, together with the

Table 3. Summary of MaxLike models used for estimating the geographic range of the short-tailed river stingray (*Potamotrygon brachyura*) in the Río de la Plata basin (excluding the Río de la Plata and lower Uruguay rivers)

Models are ranked acording to their Akaike Information Criterion (AIC) from lowest (best model) to highest (worst model). Predictors: isoT, isothermality; ac, flow accumulation; alt, altitude; wi, topographic wetness index; flv, percentage of flooded vegetation; opw, percentage of open water; ecor, ecoregion. Predictors with a '2' indicate the inclusion of a quadratic term

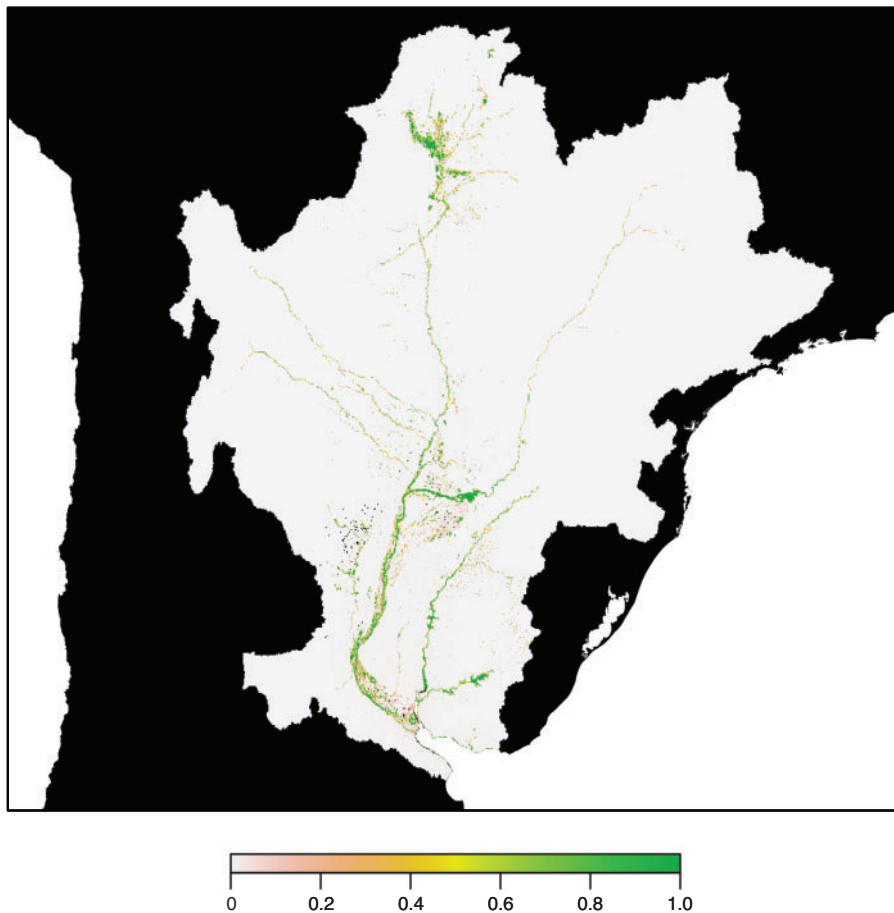| Rank	Predictors	AIC
1	ac, alt, wi, flv, opw, ecor	861.11
2	isoT, ac, alt, wi, flv, opw, ecor	861.99
3	isoT, ac, alt, wi, flv, opw, ecor, wi2	862.54
4	isoT, ac, alt, wi, flv, opw, ecor, ac2, wi2	863.62
5	isoT, ac, alt, wi, dis, flv, opw, ecor, ac2, wi2, dis2	866.92
6	isoT, ac, alt, wi, dis, flv, opw, ecor, ac2, wi2	868.43
7	isoT, ac, alt, wi, dis, flv, opw, ecor, isoT2, ac2, wi2, dis2	868.66
8	isoT, ac, alt, wi, dis, flv, opw, ecor, isoT2, ac2, wi2, dis2, flv2	870.83
9	isoT, ac, alt, wi, dis, flv, opw, ecor, isoT2, ac2, alt2, wi2, dis2, flv2	872.56
10	isoT, ac, alt, wi, dis, flv, opw, ecor, ac2, wi2, dis2, flv2	872.72
11	isoT, ac, alt, wi, dis, flv, opw, ecor, isoT2, ac2, alt2, wi2, dis2, flv2, opw2	874.91
12	isoT, ac, alt, wi, dis, flv, opw, ecor, isoT2, ac2, wi2, dis2, flv2, opw2	876.50
13	isoT, ac, alt, wi, flv, opw, wi2	884.92

Fig. 3. Probability of occurrence of the short-tailed river stingray (*Potamotrygon brachyura*) in rivers and wetlands of the Río de la Plata basin (excluding the Río de la Plata and lower Uruguay rivers), as estimated by a MaxLike model. White area: Río de la Plata basin. International boundaries are omitted to improve visualisation of the results along rivers. Map projection is Mollweide equal area.
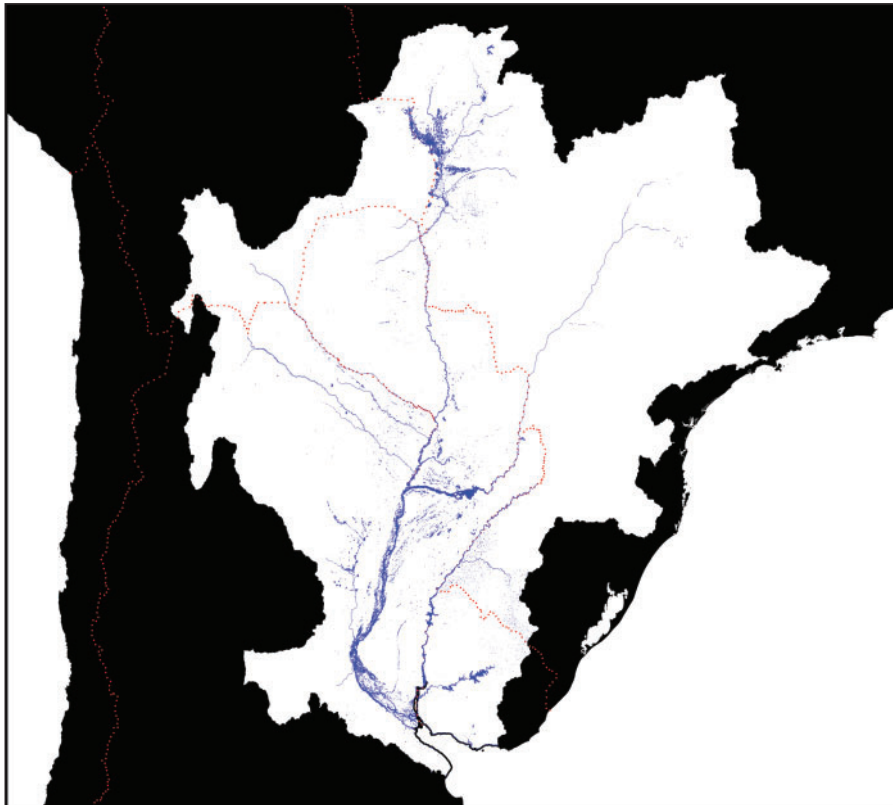
Fig. 4.   Geographic range of the short-tailed river stingray (*Potamotrygon brachyura*) in the Río de la Plata basin (excluding the Río de la Plata and lower Uruguay rivers). The geographic range results from applying a threshold maximising the sum of sensitivity and specificity to the probability of occurrence estimated by a MaxLike model. White area: Río de la Plata basin. International boundaries are shown as dotted lines. Map projection is Mollweide equal area.

Bermejo River, the most important river of the Chaco ecoregion (Monasterio de Gonzo 2003; Menni 2004). Records of *P. brachyura* are well known in the Bermejo River (Fig. 1). Conversely, the Pilcomayo lacks any record of *P. brachyura*, despite having suitable habitat for most of its lowland reach (Fig. 4). This may be a case of undersampling because other large fish species are present (and exploited) in the Pilcomayo as far up as Bolivia, such as the teleostean sorubims (*Pseudoplatystoma corruscans* and *P. fasciatum*) (Monasterio de Gonzo 2003), pacús (*Piaractus mesopotamicus*) and dorados (*Salminus brasiliensis*) (López *et al.* 2009). The ichthyofauna of the lower Salado River is similar to that of the middle Paraná (Scarabotti *et al.* 2011); in fact, there is a record of an undetermined *Potamotrygon* species found during a mass mortality of fishes in the lower Salado. The Iberá wetlands are a known habitat for other species of *Potamotrygon* (Casciotta *et al.* 2005). The Corrientes River, where *P. brachyura* is present, may act as a corridor for the dispersal of *P. brachyura* between the middle Paraná River and Iberá, as is the case for other large fishes (Waller *et al.* 2004). The Bajos Submeridionales wetlands comprise a system of highly variable water level, mainly as a result of pluriannual cycles, such as El Niño–Southern Oscillation, which has a large effect on its ichthyofauna (Pautasso and Virasoro 2011). Large teleostean fishes, such as *S. brasiliensis*

and *P. corruscans*, have been recorded in these wetlands, but mostly after large floods during El Niño years (Pautasso and Virasoro 2011), and a freshwater stingray of the *Potamotrygon motoro* species complex has been recorded in the area (López *et al.* 2008). We hypothesise that *P. brachyura*, like *S. brasiliensis* and *P. corruscans*, could be present in the Bajos Submeridionales only during high water levels.

In the RdlP, *P. brachyura* appears to be restricted to a narrow strip adjacent to the coastline. This pattern may be related to the distribution of the benthic fauna, a potential food resource of *P. brachyura*. In the RdlP, both density (Rodrigues Capítulo *et al.* 2002) and species richness (Brazeiro *et al.* 2003) of benthic organisms are highest close to the shore and lowest in the middle of the river. We hypothesise that this spatial pattern arises as a response of *P. brachyura* to a general increase in benthic biomass towards the coast that may attract other benthic-feeding fishes as well. An abiotic factor that affects the abundance of benthic organisms in the RdlP is the percentage of sand in the sediments (Rodrigues Capítulo *et al.* 2002). This same factor is usually an important determinant of the abundance of many *Potamotrygon* species (Shibuya *et al.* 2009; Garrone-Neto and Uieda 2012). An alternative hypothesis is that percentage of sand, rather than benthic fauna abundance itself, determines the congruence between the distribution of *P. brachyura* and the
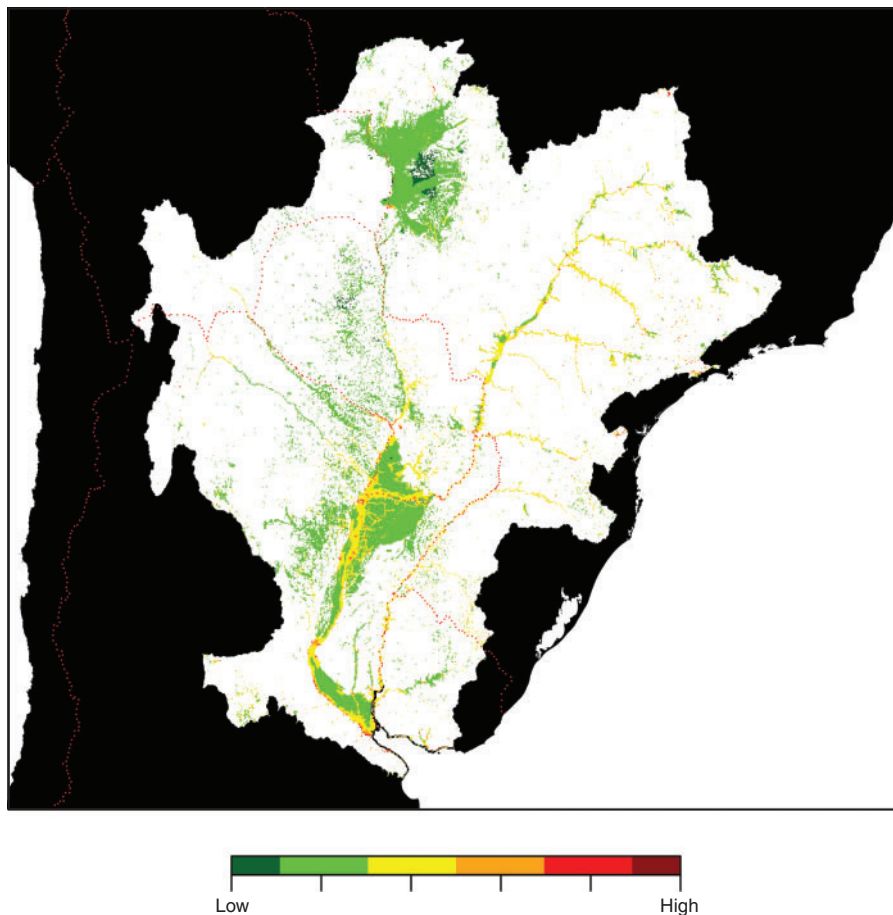
Fig. 5. Habitat modification threat levels for aquatic habitats of the Río de la Plata basin (excluding the Río de la Plata and lower Uruguay rivers). Data are taken from Wildlife Conservation Society (WCS) and Center for International Earth Science Information Network, Columbia University (CIESIN) (2005). White area: Río de la Plata basin. International boundaries are shown as dotted lines. Map projection is Mollweide equal area.

benthic fauna. A similar interplay between sediment type and benthic prey distribution has been observed for another batoid of the estuarine and marine zones of the Río de la Plata (Barbini *et al.* 2011), suggesting that sediment type may be an important factor affecting chondrichthyan predators in this ecosystem dominated by soft bottoms.

Despite suitable habitat being available, *P. brachyura* has not been able to invade the upper Paraná River basin, which may be indicative of a low reproductive output. After the completion of the Itaipú hydroelectric dam in 1982, near the triple border between Argentina, Brazil and Paraguay, a natural barrier between the Upper and Lower Paraná freshwater ecoregions – the Guairá or Sete Quedas falls – was obliterated and a massive exchange of fauna between both ecoregions started (Júlio Júnior *et al.* 2009; Vitule *et al.* 2012). This led to an invasion of the Upper Paraná by multiple fish species of the more diverse (Albert *et al.* 2011) Lower Paraná ecoregion (Júlio Júnior *et al.* 2009; Vitule *et al.* 2012). Two or three species of *Potamotrygon* have established viable populations in the newly invaded ecoregion (Garrone-Neto *et al.* 2007, 2014; da Graça and Pavanelli 2007; Loboda and de Carvalho 2013). However,

P. brachyura has been unable to reach the Upper Paraná ecoregion so far, despite having been recorded close to the Itaipú dam (Fig. 1). We hypothesise that this may be indicative of a slow life history that translates into slow population dynamics. The species that have invaded the Upper Paraná ecoregion are all much smaller than *P. brachyura*, a trait associated with a fast life history, which is a characteristic of invasive fish species (Helfman 2007). An alternative explanation could be that *P. brachyura* has a lower dispersal ability than the invasive *Potamotrygon* species. Although we cannot reject this possibility completely, dispersal ability, however, tends to be associated positively with body size (Jenkins *et al.* 2007), which suggests this is not the case.

Assessment of threats

The importance of habitat modification as a threat differs among the RdlP and UP. Habitat modification is a problem for *P. brachyura* in the RdlP. This is exacerbated by the strictly coastal distribution of *P. brachyura*. Coastal areas of the RdlP, especially the southern (Argentinian) shore, are among the most
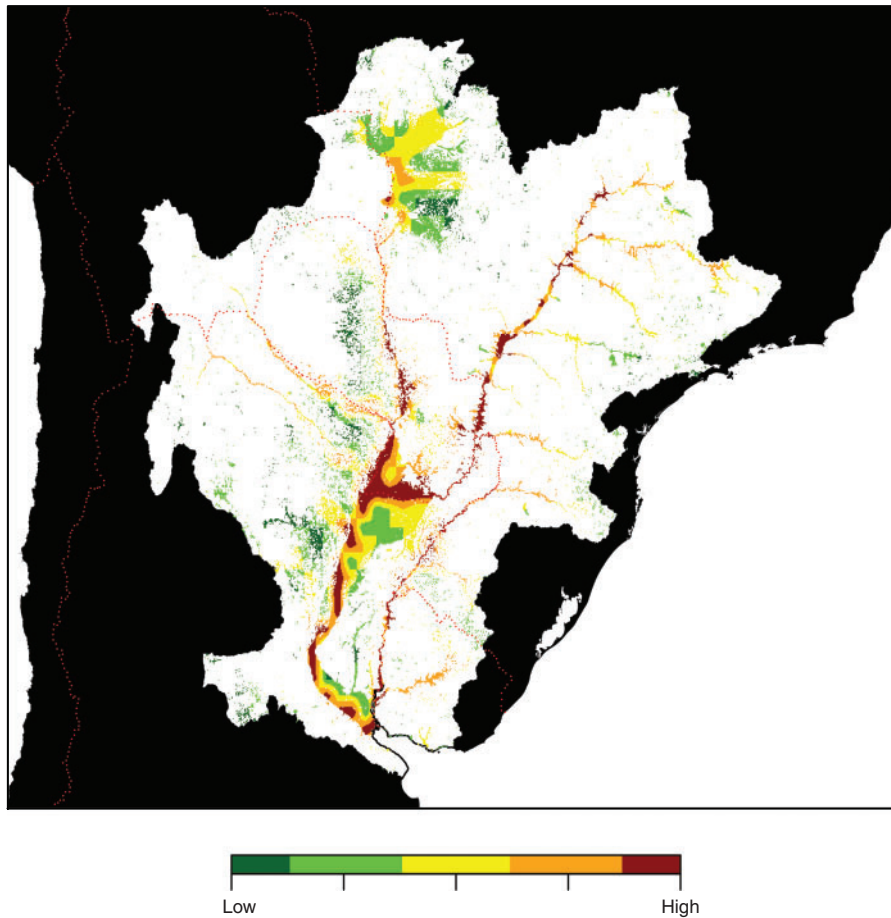
Fig. 6. Fishing pressure threat levels for aquatic habitats of the Río de la Plata basin (excluding the Río de la Plata and lower Uruguay rivers). Data are taken from Vörösmarty *et al.* (2010). White area: Río de la Plata basin. International boundaries are shown as dotted lines. Map projection is Mollweide equal area.

modified and polluted in the basin because this area contains large industrialised urban conglomerates (Murguía *et al.* 2006; Barletta *et al.* 2010). For example, the concentration of hydrocarbon and polychlorinated biphenyls in detritivorous fish from the southern shore of the RdlP was 1–2 orders of magnitude higher than that of fish from the lower Paraguay River (Speranza *et al.* 2012). Access to the main ports in the RdlP is maintained through dredging, which destroys the physical structure of the benthic ecosystem. Dredging intensity in the RdlP is highest in the coastal zones of the innermost RdlP (Brazeiro *et al.* 2003), which overlaps with the distribution of *P. brachyura* in the area.

Habitat modification in the UP appears not to be a stressor for *P. brachyura* at present. This is because of the fairly well conserved and mostly unmodified Paraguay–middle Paraná River axis. This riverine axis contains one of the largest continuous wetland areas in the world (from the Pantanal, in the upper Paraguay River, to the huge floodplains of the middle and lower Paraná River), has a rather low human density through most of its area, and has no dams along its 3700 km (de Resende 2003; Quirós *et al.* 2007). In fact, it has been proposed as a baseline for the restoration of other large disturbed floodplain rivers (Nestler *et al.* 2007). With some

exceptions, the region still conserves most of its original wetland-dependent fauna, including large vertebrates, such as two species of caimans (*Caiman latirostris* and *C. yacare*), yellow anacondas (*Eunectes notaeus*), and the mammalian capybaras (*Hydrochoerus hydrochaeris*) and swamp deer (*Blastocerus dichotomus*) (Bó 2006; Giraudo and Moggia 2008). Among fishes, although the mean size and abundance has decreased in many areas of the riverine axis (Quirós *et al.* 2007), there are still areas within the region where the largest, most sensitive species persist, such as, among catfish, two species of sorubim (*P. corruscans* and *P. fasciatum*), and the manguruyú or jau (*Zungaro jahu*), and, among characoids, dorados (*S. brasiliensis*) and pacú (*P. mesopotamicus*) (Quirós *et al.* 2007). Our finding for *P. brachyura* therefore appears to be congruent with trends for other large fishes and vertebrates of the Paraguay–middle Paraná axis.

Nevertheless, the environmental situation of the Paraguay–middle Paraná riverine axis is far from safe in the mid- and long term. The hydrological cycle of floods, a process of capital importance in the life cycle of most of the region's biota (Junk *et al.* 1989), has been affected by the cascade of dams built in the upper Paraná River (Quirós *et al.* 2007). To present day, this

effect has been one of modulation of the flood pulse for the middle Paraná River because dams retain water during high-water seasons and release it slowly during low-water periods; this results in a decrease in the variability of the flood pulse, both spatially and temporally (Quirós 2004; Quirós *et al.* 2007). In addition, these dams interrupted the long-distance movements of migratory fish species, which are also the largest and most valuable for fisheries (Quirós 2004; Quirós *et al.* 2007; Baigún *et al.* 2011). These effects are rather indirect as compared to the direct effect that planned infrastructure projects will have on the Paraguay–middle Paraná axis if completed. There are several hydropower dam projects on the Paraná River in Argentina and one international transportation megaproject ('Hidrovía Paraná–Paraguay') that will allow navigation between Brazil, Bolivia, Paraguay and Argentina through the Paraguay–middle Paraná axis. A major disruption of the flood pulse and the loss of the continuity of the wetland corridor are expected if such projects are consummated (de Resende 2003; Baigún and Oldani 2006; Junk *et al.* 2006; Peteán and Cappato 2006; Quirós *et al.* 2007). Also, the expansion of the agricultural frontier during the last decade, mainly for soybean crops, has brought the problem of land conversion and agrochemical pollution to these wetlands (Bó 2006; Quirós *et al.* 2007; Giraudo and Moggia 2008).

Currently, fishing pressure appears to pose a more direct threat for *P. brachyura* than habitat modification in the UP because large areas of the predicted distribution of *P. brachyura* overlap with zones of high fishing pressure. Some areas of the Río de la Plata basin, especially those where strict regulations are imposed to conserve recreational fisheries, such as the Pantanal and the confluence of the Paraná and Paraguay rivers (de Resende 2003; Quirós *et al.* 2007), still harbour a fairly large number of large fishes. However, there is increasing evidence that fishing effort is beyond sustainable levels in many areas of the basin. This evidence includes a decline in the abundance of large predatory fishes (de Resende 2003; Baigún and Oldani 2006; Quirós *et al.* 2007), a decrease in both mean and maximum size of the main target species, an excessive exploitation level (the catch exceeds three times the maximum sustainable yield in some years) (Baigún and Oldani 2006; Baigún *et al.* 2013), and an overcapacity of the fishing industry (Peteán and Cappato 2006). To what extent the exposure of *P. brachyura* to this high fishing pressure will result in a negative effect on its population(s) will be determined by the species' sensitivity to fishing mortality. This sensitivity depends on the biological characteristics of *P. brachyura* (e.g. its life-history and population parameters) and on the actual proportion of the fishing effort that catches the species. Although it is currently not possible to estimate this sensitivity because of lack of data, it is advisable to take a precautionary approach for two main reasons. First, a large maximum size, one of the most evident traits of *P. brachyura*, is known to be positively correlated in chondrichthyans to both a high age at maturity and a high extinction risk (García *et al.* 2008; Hutchings *et al.* 2012). Second, catches of *P. brachyura* appear to be rather common, particularly in the southernmost part of its range (Fig. 1), suggesting that fisheries could pose a threat to the species if it is sensitive enough.

The conservation of *P. brachyura* may also bring conservation opportunities for the whole Río de la Plata basin. Owing to their popularity, some freshwater elasmobranchs have been proposed as flagship species (Fowler 2002), i.e. charismatic species used to stimulate conservation awareness (Barua 2011). *P. brachyura* may also serve as an umbrella species for the Río de la Plata basin. Umbrella species have habitat and area requirements so large that their conservation will necessarily include other species as well (Barua 2011). Accordingly, we have shown that *P. brachyura* has a geographic distribution covering a high proportion of the basin's environments. The large areas of fairly well conserved wetlands in the Río de la Plata basin suggest that there is still an opportunity for the conservation of *P. brachyura* and the ecosystem it inhabits.

Acknowledgements

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