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Bright spots for research and conservation of the largetooth sawfish *Pristis pristis* in Colombia and Panamá

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ABSTRACT: Sawfishes are considered one of the most endangered families of fishes globally. Their diadromous ecology and vulnerability to fishing nets have brought most populations to the brink of collapse. Conservation of surviving populations is hindered by limited knowledge of historic and contemporary distribution. Colombia and Panamá are 2 of 22 countries considered as high priority for the development of species-specific national legal protection of the Critically Endangered largetooth sawfish *Pristis pristis*. To construct a baseline for the temporal and spatial distribution of the largetooth sawfish in Colombia and Panamá, we collected historical records from museum databases and literature over the past century, analysed available small-scale fisheries landings databases, and conducted interviews with fishers in 38 locations. We found 248 records of sawfish occurrences across both countries between 1896 and 2015, with 69% of the records from before 2000. The declining frequency of observations was corroborated by fishers, who reported fewer sawfish sightings and catches over the last 20 yr. Results from a regression model of total length and observed date suggest that the maximum size of observed sawfish individuals has also declined over time. We use location data from sawfish records to identify potential 'bright spots' that may foster remaining populations of sawfish. The locations of sawfish records were broadly characterised as remote areas with high mangrove forest cover. Given the length and cultural diversity of the Pacific coastlines of Colombia and Panamá, our findings provide important guidance to implement rapid conservation and fisheries interventions in these priority areas and highlight geographical gaps in knowledge for further work.

KEY WORDS: Pristidae · Elasmobranchs · Small-scale fisheries · Historical ecology · Biological collections · Archaeozoology · Mangroves · Traditional knowledge

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1. INTRODUCTION

All 5 extant species of sawfish are listed by the IUCN as Endangered or Critically Endangered with a high risk of extinction (Dulvy et al. 2016), making them the most threatened family of marine fishes at the time of writing (Dulvy et al. 2014, Braulik et al. 2020). Sawfishes, characterised by their tooth-studded rostra and large body size, are distributed globally in the tropics and subtropics, inhabiting shallow coastal waters such as estuaries, mangrove areas, and rivers (Harrison & Dulvy 2014). Sawfish diadromy has been widely documented in rivers of Central America as well as natural (Lake Cocibolca, Nicaragua) and man-made (Lake Bayano, Panamá) lakes (Thorson 1976, Cooke 1994).

Considerable research has documented the vulnerable status, declines, and disappearances of sawfish populations from many coastal areas around the world, such as Papua New Guinea (White et al. 2017), Guinea-Bissau (Leeney & Poncelet 2015), the USA (Seitz & Poulakis 2006), Bangladesh (Haque et al. 2020), and the Mediterranean Sea (Ferretti et al. 2016). Their widespread decline has been associated with their high catchability in fisheries, given their easily entangled rostra (Simpfendorfer 2000), the extensive loss of their nursery habitats (Hossain et al. 2015, Haque et al. 2020), their high value in the fin trade market (McDavitt 2014), and their low intrinsic rates of population increase (Simpfendorfer 2000).

Long-term human impacts on marine species and ecosystems are widely recognized (Jackson et al. 2001). Historical data are important to understand the population dynamics of declining or locally extirpated species (McClenachan et al. 2012, Turvey et al. 2015) and to set appropriate targets for recovery (Thurstan et al. 2015, Engelhard et al. 2016). Often, the first step in developing any conservation management strategy is to establish a picture of the resource before human disturbance, but it is argued that conservation management should acknowledge and incorporate changing human perceptions of land and resources over time in addition to merely pristine targets (Alagona et al. 2012).

The historical and contemporary status of sawfish populations in Colombia and Panamá is largely unknown, due to the lack of detailed information on observations or fishery catches, particularly for sharks and rays in the region. However, the Pacific coasts of Panamá and Colombia present suitable ecological habitat for sawfish, which combined with the low human population density may harbour remnant populations of sawfish. The globally distributed largetooth sawfish *Pristis pristis* (Linnaeus, 1758) is known to have occurred historically in the southern Caribbean (Gómez-Rodríguez et al. 2014) and on the Pacific coasts of Colombia and Panamá. *P. pristis* is the largest species of the sawfish family, with a maximum recorded length of 705 cm (Devadoss et al. 1989), and can live up to 36 yr (Peverell 2009). This species is euryhaline, with adults preferring shallow marine and estuarine environments and juveniles occurring in rivers (Thorson 1982). It is characterised by late age at maturity (8–10 yr) and low fecundity (max. litter size of 20), resulting in a low intrinsic rate of population increase (Simpfendorfer 2000, Moreno Iturria 2012). No recent biological or ecological information exists for *P. pristis* in Colombia and Panamá, since it is an extremely rare species in the area and therefore difficult to assess and research. The species is known to be locally extinct in 27 of the 75 countries where it was historically present (Faria et al. 2013, Dulvy et al. 2016, Mendoza et al. 2017). In its native Caribbean range, *P. pristis* is thought to be locally extinct (Gómez-Rodríguez et al. 2014). In the eastern tropical Pacific, it could already be locally extinct along a large part of its original distribution from Mexico to Perú (Harrison & Dulvy 2014).

As of June 2019, the governments of Colombia and Panamá agreed to impose strict national protections for all sawfish species (prohibited destruction, disturbance, exploitation, possession, or trade) and cooperate regionally to foster the recovery of populations through their classification as critically endangered under Annex II of the Specially Protected Areas and Wildlife (SPAW) Protocol. Colombia and Panamá are 2 of the 22 countries categorised as high priority for the development of species-specific national legal protection of sawfishes, given the scarcity of research and the availability of potential sawfish habitat (Harrison & Dulvy 2014).

The present study aimed to identify potential areas of extant populations, 'bright spots', of *P. pristis* in Panamá and Colombia. By consolidating observation records from a variety of sources since records began, we identify historical changes in occurrence and distribution. Additionally, by combining this with targeted interviews in key fisheries landing sites, we sought to identify the primary drivers of change. Additionally, we explore temporal shifts in *P. pristis* total length to determine if populations in Colombia and Panamá show size structure decreases similar to commercially targeted fisheries species (Sibert et al. 2006, Zgliczynski & Sandin 2017). Given the combined Pacific coastline of both countries extends more than 3000 km, this study aimed to provide guidance and locations to governments and stakeholder agencies to

focus conservation efforts in the region. This serves to support their new commitments under the SPAW Protocol to foster the protection and recovery of populations of critically endangered sawfishes.

2. MATERIALS AND METHODS

2.1. Study area

Colombia and Panamá are countries characterised by their high biodiversity and forest coverage, sharing regions of similar ecological and biogeographical features and special conservation value (Martin et al. 2016), such as the Chocó-Darién corridor. Both countries have Pacific and Caribbean coastlines. Their Pacific coasts are characterised by estuarine lagoons, rainforests, high cliffs with pocket beaches, rocky shores, long sand beaches, mangrove swamps, and mudflats (Lacerda et al. 1993). The Chocó-Darién ecoregion is considered to have one of the highest rates of annual rainfall in the world (ca. 8000–13 000 mm), feeding numerous river deltas and estuaries. In contrast to the Caribbean coast, the Pacific coast exhibits extensive mangrove habitat with 4 designated Ramsar wetlands: (1) Golfo de Montijo, (2) Bahia de Panamá, (3) Punta Patiño (Darién), and (4) Baudó Delta (Chocó, Colombia) (https://www.ramsar.org/). Most villages along this coastline rely heavily on small-scale and semi-industrial fisheries, subsistence hunting for wild game, and agriculture for their livelihoods and food security. Poverty is widespread, and there is high reliance on natural resources, particularly mangroves (Trejos et al. 2007). The population along the Pacific coast is composed of mestizos, Afrodescendants, and Indigenous peoples from diverse tribes (with the Emberá being most dominant), sometimes inhabiting remote and isolated villages scattered in the rainforest (Díaz & Caro 2016).

2.2. Historical sawfish records

A comprehensive literature review was undertaken in Google Scholar using the scientific and common names of sawfish species in Spanish and English. Sightings and captures of sawfish, or other documented evidence of sawfish presence in Colombia and Panamá were searched for in national and international online databases (Table S1 in Supplement 1 at www.int-res.com/articles/suppl/n046p147_supp1.xlsx). Records found in the Global Biodiversity Information Facility were cross-referenced with museum collections to collect any additional information on capture location and date and morphometrics of the specimens where available. We also obtained records from the International Sawfish Encounter Database (ISED), hosted by the Florida Museum of Natural History.

Relevant government departments and non-governmental organisations in both countries were visited or contacted to find recent and archaeozoological records documented in their databases (Table S1). Museums in Colombia and Panamá holding sawfish specimens were visited or contacted to collate information from collection metadata (Table S1). Museum collection managers, curators, and elasmobranch researchers were consulted directly to request information about possible specimens or rostra, literature, or expedition reports that could contribute more data, such as detailed capture location, year of capture, method of capture, and specimen size and sex. Where preserved specimens existed and could be accessed, we measured morphometric variables such as total length (for full-body specimens), total rostrum length, and the number of teeth.

2.3. Fisheries catch records

Available fisheries landings data sets in Colombia and Panamá were reviewed and explored for sawfish landings records. In Colombia, landings data were collected by Fundación MarViva in a participative fisheries monitoring program between 2010 and 2013 (López-Angarita et al. 2018a). For the southern Colombian Pacific coast, the landings database compiled as part of the US Agency for International Development Bioredd+ fisheries program 2012 to 2014 (Tilley & Box 2014, Tilley et al. 2018) was consulted for sawfish records. In Panamá, landings data were obtained through data-sharing agreements with the Universidad de Panamá. These data were collected by the Panamá government's fishery resources authority, Autoridad de Recursos Pesqueros de Panamá, and are a record of fishery landings from 15 villages across the Gulf of Montijo between 2008 and 2012 (López-Angarita et al., preprint https://doi.org/10.1101/2021.10.07.463581).

2.4. Interviews

The surveyed area encompassed the Pacific coasts of Panamá and Colombia. In Panamá, we surveyed communities across an area that stretches 772 km

from the estuaries of Pedregal (Chiriquí, Panamá) to Mariato in the estuaries of the Gulf of Montijo, continuing to the Aguadulce District, and finishing in Garachiné (Darién, Panamá). In Colombia, we interviewed communities in the northern Chocó region between Punta Piña and Arusí. In total, we surveyed 38 communities (Fig. S1 in Supplement 2 at www.int-res.com/articles/suppl/n046p147_supp2.pdf). Interview sampling was focused on the Pacific coasts of Colombia and Panamá (Fig. S1), as the types of ecosystems and habitats are favourable for largetooth sawfish, and previous research (using literature searches and interviews) suggested they are locally extinct in the Colombian Caribbean (Gómez-Rodríguez et al. 2014, Caldas et al. 2017). Due to budgetary constraints, interviews were not conducted in the southern departments of the Colombian Pacific coast (Valle del Cauca, Cauca, and Nariño), but fisheries landings records were obtained and analysed from these areas.

Semi-structured interviews were conducted by 2 trained scientists between 2015 and 2016 (Text S1). Local fish workers (i.e. fishers, traders, fishing cooperative representatives) and experts were asked to provide information on sawfish records or observations in or near their local area, according to their knowledge and experiences. Fishers with more than 15 yr of fishing experience were considered local experts and were interviewed to collect fishers' ecological knowledge data. Surveys were designed to gather information on (1) past and current abundance of sawfishes within the region, (2) perceived causes of decline, and (3) the cultural and economic importance of sawfish in their community. Photos of sawfishes were used to assess the ability of fish workers to identify the species, to record local names in use, and to prompt insights or records of catches and locations for the species. Printed maps were used to allow fish workers to identify specific areas of interest if they were too distant to show data collectors in person. Fish workers were asked to describe their encounters or sightings of sawfish. Where possible, the date, locality, size, and behaviour of the individual were recorded; however, if respondents struggled with specific details (for example from very old encounters), only specific data about their last sighting were used. Interviews were filmed with the informed consent of participants.

2.5. Data management and analysis

Records of *Pristis microdon* and *P. perotteti* were treated as largetooth sawfish *P. pristis* following the latest taxonomic reclassification (Faria et al. 2013). Any sawfish records from the Pacific coast were treated as *P. pristis*, whereas for the Caribbean coast, records were maintained as either *Pristis* sp., *P. pristis*, or *P. pectinata*. To clarify the process of sorting historical records, the term specimen is used to refer to records in museum collections. If records could be associated with location and date information, then they are termed occurrences. Non-interview observations refer to sawfish occurrences recorded or recollected from fishers and scientists as anecdotal information that were not recorded in structured interviews. Interviews were transcribed and coded by specific themes of interest. Qualitative analysis of interview responses was then performed using Nvivo software (v. 11.1.1) to provide summary statistics of keywords and themes from the recorded answers.

Fisheries landings databases were filtered by species and location to provide a summary list of all sawfish captures along with capture date and location. The occurrences of sawfish in Panamá and Colombia from bibliographic sources, museum specimens, and interviews, with associated coordinates, were mapped using QGIS v. 3.8.0.

The extent of occurrence and the reduction of extent of *P. pristis* in the eastern tropical Pacific were determined using georeferenced observations grouped into historical (1900–2009) and contemporary (2010–2015) bins. Kernel density interpolation in QGIS (v. 3.4.11 Madeira and Heatmap plugin v. 0.2) was used to estimate probability densities for the habitat ranges of sawfish based on the extent of occurrence and not abundance or population density. Previous studies have described the home range of largetooth sawfish in riverine areas and estuaries, yet there is limited understanding of sawfish habitat ranges and their connectivity in coastal areas. Thus, we considered the habitat range to be the home range used by each individual. We made no inferences about habitat resources or specific animal behaviour other than the depth range as a biological boundary for distribution. Habitat range per observation was tested at 50 and 100 km (0.45° and 0.9°, respectively) following suggested habitat ranges in Dulvy et al. (2016) and Last et al. (2016). Depth was used as a biological boundary and a predictor for sawfish presence–absence for 2 scenarios: (1) 0–50 m depth, and (2) 0–100 m. Bathymetry contours were compiled from GEBCO (2020). Marine protected areas were mapped using cartography from Fundación MarViva, and where necessary, polygons were created manually.

2.6. Temporal shifts in sawfish size

Changes in sawfish size over time were explored with a (Bayesian) regression model using records for which total length and date were available. These records were supplemented with estimations of total length using the allometric relationship between rostra and the total length (Text S2, Fig. S2). These records were further filtered to include only the largest total length measurement for a given year or source type combination. This was done because the limited number of records in any given year makes it unlikely that the data provide a complete picture of the size distribution changes. Response to exploitation has been shown to be greatest for larger fish within size classes (Graham et al. 2005), and many of the records are likely to be neonate and juvenile individuals and so may offer little information about changes to population size structure.

The response variable in the model was total length, and the explanatory variable was the year of record. The year of record was scaled to have a zero mean and unit variance prior to inclusion in the model. In addition, to control for potential biases in the data, random intercepts for the country of record and the source of the record (museum collection, literature, ISED, interview and non-interview observation) were calculated. Total length was modelled using a binomial distribution in preference to a Poisson distribution because this distribution is ideal for modelling integer values within a specified range; this was important in this case because total length has an upper bound. This upper bound was set at 120% of the length of the largest measured specimen. To account for overdispersion in the data, each observation was included as an additional random intercept. A weakly informative prior based on a Student's *t*-distribution with 3 degrees of freedom, a median of zero, and a scale of 2 was used for all model coefficients. The Bayesian model was fitted using brms 2.14.4 (Bürkner 2017, 2018), which uses a Hamiltonian Markov chain Monte Carlo algorithm implemented in Stan (Stan Development Team 2021). The model was fitted using 4 chains of 5000 iterations each (including 2500 for warm-up). Trace plots of the model chains suggested that the chains were well mixed and the model converged appropriately. Accordingly, the potential scale reduction factor, R-hat, of all our estimates was 1.00. Model convergence was assessed using trace plots, and model specification was assessed using posterior predictive checks. These checks showed that the distribution of simulated data from the posterior predictive distribution resembled the observed data.

3. RESULTS

A total of 248 records of sawfish encounters from 1896 to 2015 were compiled through museum specimens (59), ISED (24), literature (55), observations of interviewed fishers (95), and other non-interview observations (15) (Figs. 1 & 2). Of these, 162 records belong to Panamá (Pacific: n = 147, Caribbean: n = 4, not specified: n = 11) and 86 to Colombia (Pacific: n = 51, Caribbean: n = 32, not specified: n = 3). Thirty-four records had no accompanying date or location

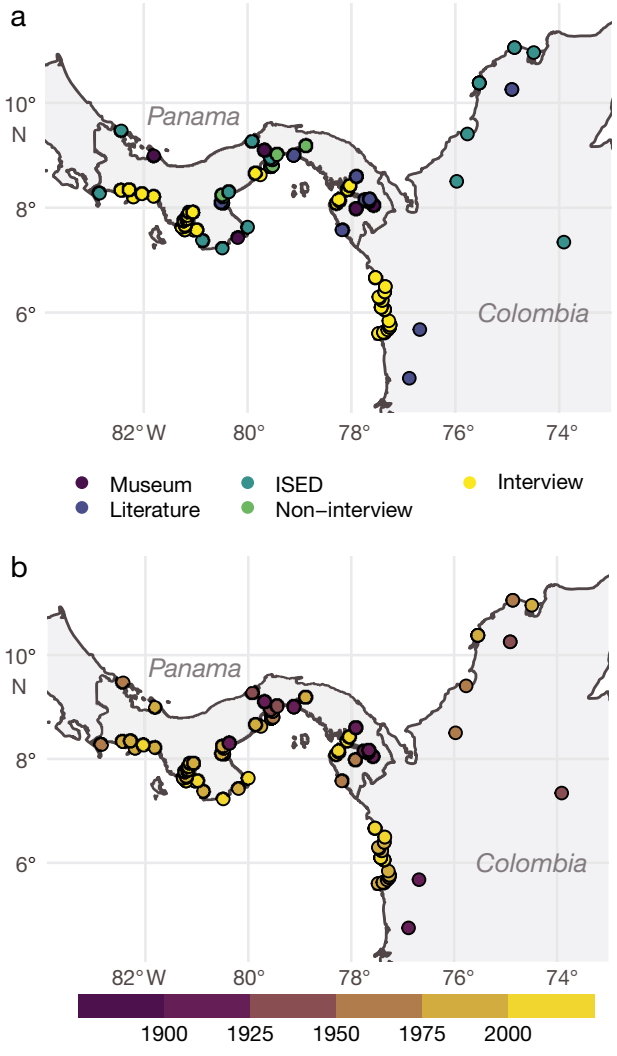

Fig. 1. Distribution of largetooth sawfish *Pristis pristis* and *Pristis* sp. occurrences by (a) source type, and (b) reported year in Colombia and Panamá. Yellow dots in the upper panel (a) show communities where interviews were undertaken between 2015 and 2016. ISED refers to records obtained from the International Sawfish Encounter Database, hosted by the Florida Museum of Natural History. The dot situated in the middle of Colombia corresponds to an occurrence found 600 km upstream in the Magdalena River in 1945

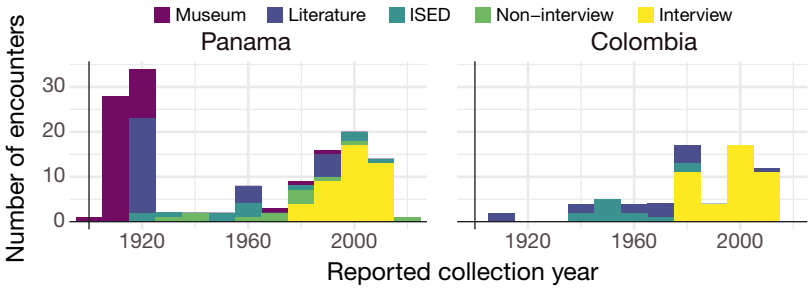

Fig. 2. Counts of sawfish observations in Panamá and Colombia (including Pacific and Caribbean coasts) according to record source type, location, and year. ISED refers to records obtained from the International Sawfish Encounter Database, hosted by the Florida Museum of Natural History

information. In Colombia, 65% of records date from before the year 2000, and this period also represents the majority of occurrences recorded in Panamá, with 82%.

The total number of records with date and location data from the Pacific region across Colombia and Panamá was 188. Of these, 71% correspond to observations before the year 2000, while 20% were reported between 2000 and 2009 and 9% since 2010 (Fig. 2). From the Caribbean region, 38 observations were obtained, of which 20 records had date and location information, 15 were largetooth sawfish *Pristis pristis*, 7 were smalltooth sawfish *P. pectinata*, and the remaining were only catalogued to the genus *Pristis* sp. The largetooth sawfish *P. pristis* is hereafter referred to as sawfish.

3.1. Historical sawfish records (literature and collections)

Most specimens (wet and dry) found in collections and museums were housed outside Panamá and Colombia, with most from the Field Museum of Natural History Fish Collection (Chicago, IL, USA) (n = 13), the Smithsonian Institution's National Museum of Natural History (NMNH) (Washington, DC, USA) (n = 17), and the Natural History Museum (London, UK) (n = 10) (Table S2). ISED yielded 24 records, of which all but one had accompanying date and location metadata. Most of the occurrences found from the Pacific region belonged to Panamá, most of which were specimens from 2 biological expeditions (ichthyofaunal assessments) in 1912 (Meek & Hildebrand 1923) and 1924. Four records were from Colombia, 1 recorded as an observation in Guajira (Caribbean coast) and another as a specimen in NMNH without a specified location. The other 2 records found in Colombia were from the Sistema de Información Ambiental Marina (INVEMAR 2021) database for *P. pectinata* and *P. perotteti*, but no further information accompanied these records.

From 59 records found in bibliographic searches of academic and grey literature (magazines and books), 4 belonged to archaeozoological evidence found in Colombia and Panamá. The rest of the records were obtained from published literature dating back as far as 1890. For all of these, information regarding location, species, and an approximate date were available. Of these 59 records, 42 belonged to *P. pristis*, 7 to *P. pectinata*, and 10 were only identified to genus. Morphological information was available for 30 records.

We contacted or personally visited 19 museums and zoological collections in the USA and Europe, 7 in Colombia, and 3 in Panamá. Morphometric data were taken from 6 sawfish specimens found in Colombia and 9 in Panamá. Two of the specimens from Colombia did not have any accompanying information, but the whole specimen was available. Specimens from Panamá lacked specific location data and consisted mainly of rostra. Information provided by the curators confirmed that specimens were brought to the museums before 2000.

3.2. Fisheries catch records

The database of small-scale fisheries landings from the northern Chocó region, Colombia, between 2010 and 2013 represented 36 448 fishing trips. The main gear types represented in the landings were hand line, long line, gill net, spear gun, beach seine, and manual collection of molluscs. Of 449 reported fishing grounds (i.e. sites where people regularly fish), 32 were located inside mangroves, and 55% of the 284 identified species exhibited life histories that are strongly connected to mangrove habitat. However, no sawfish captures were reported. The 3 years of data available for small-scale fisheries in the Gulf of Montijo (Panamá) between 2010 and 2012 showed that sampling frequency and effort varied widely among the 14 villages sampled with large data gaps, some with entire years missing. Total catch volume across the 3 years was 203 tonnes, and the most important fishery was 'revoltura', a local classification for a mixture of low-value species (e.g. weakfish, drums, croakers) caught with

gill nets in nearshore mangrove and estuarine areas. No sawfish captures were reported. The southern Colombian Pacific coast database also recorded no sawfish captures.

3.3. Interviews

In total, 106 interviews were conducted across Colombia (n = 54) and Panamá (n = 52) in 38 locations (Table 1, Fig. S1). One hundred of the respondents were males, and 6 were females. The mean number of years fishing (±SD) for all respondents was 36.5 ± 12.5 yr. The youngest respondent was 25 yr old, and the oldest was 75 yr old.

Images of the largetooth sawfish were widely recognized by fishers and fish workers along the Pacific coasts of Colombia and Panamá, with 97% of respondents throughout the region correctly identifying the species. Local names for *P. pristis* in Colombia used by fish workers were 'pez sierra' (sawfish), 'pez espada' (swordfish), and 'guacapa'. In Panamá, interviewees referred to the species as 'pez espada' and 'pejapa'. Eighty-six percent of respondents had seen a sawfish themselves, and even if they had not personally caught one, most knew someone who had. Sixty-six percent of respondents reported a decrease in the abundance of sawfish in their lifetimes. Twenty-eight percent of interviewees mentioned gill nets as possible reasons for sawfish decline; others suggested overfishing in general (16%), extinction (3%), and habitat degradation (2%) as additional reasons. Gill nets were highlighted as a particular threat because sawfish rostra become easily entangled, and some respondents recounted incidents of injury and fear while trying to extricate sawfish from their nets. In most locations, sawfishes had not been seen in more than 10 yr.

Just over one-third of interviewees (38%) said they considered sawfishes to be very strong and dangerous animals that cause harm with their teeth or even attack and break fishers' boats. Sawfish were never stated to be the target species of any fisher, and reported captures were perceived as accidental, opportunistic, and even troublesome for fishers overall. Fish workers stated that they would usually keep the rostra of killed sawfishes as ornaments in their homes, but only 1 rostrum (45 cm) was discovered during field sampling in the community of Punta Alegre (Darién, Panamá), and fishers confirmed it was captured in 2015. Some interviewees claimed that in recent years many of the older rostra specimens had been purchased by visiting tourists or buyers. When asked their perceived reason for buyers' interest in these rostra, 43% of interviewees stated it was merely decorative. For recent sawfish sightings, fishers mentioned 2 main locations: in Panamá, the Darién region and the Bahía de Chame (La Chorrera region), and in Colombia, the Utría National Park and Golfo de Tribugá.

Table 1. Number of interviews and communities by region and country conducted between 2015 and 2016. Locations of the communities can be seen in Fig. S1 in Supplement 2

Country	Region	No. of communities	No. of respondents
Panamá	Gulf of Chiriquí	5	11
	Gulf of Montijo	12	27
	Darién	4	10
	West Panamá City	4	4
Colombia	Northern Chocó	13	54

3.4. Temporal shifts in sawfish size

The relationship between rostrum and total length for the largetooth sawfish *P. pristis* was approximately isometric (Text S2, Fig. S2), with an estimated allometric coefficient of 0.9 between these 2 metrics (90% credible interval [CI]: 0.83–1). There was a 92.8% probability that the total length of the largest observed sawfish individuals (*P. pristis*) decreased between 1896 and 2016 (Fig. 3a, Tables S3 & S4). The median rate of this decrease was 5% per decade (90% CI: −0.8 to 12.1%; Fig. 3b). We found no substantial differences between the intercepts of different record sources, whether we include all records or just those with the largest individuals (Text S3, Fig. S3).

3.5. Spatio-temporal analysis

A total of 150 occurrences from the Colombian and Panamá Pacific region that included date and location data were mapped for further spatial analysis. Occurrences from Panamá were first reported at the beginning of the 20th century and were mostly composed of records collected during biological expeditions in the first part of the century. In Colombia, reporting only started in the 1980s, and most records corresponded to individual reports made by interviewees.

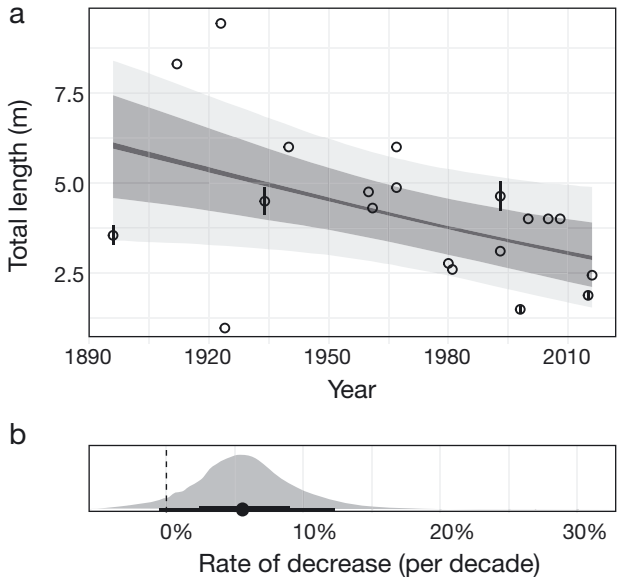

Fig. 3. Decline in maximum length of largetooth sawfish *Pristis pristis* over time. (a) Dots indicate length of records included in the model; vertical bars indicate the SE of total lengths estimated from rostrum length. Grey bands indicate 66 (light grey) and 90% (dark grey) credible intervals. (b) Distribution of the rate of decrease in total length per decade. The dot depicts the median value, and black lines correspond to 66 (thin lines) and 90% (thick lines) credible intervals

Occurrences of sawfish encounters in the last century were relatively rare, and over 55% of the records were reported from 3 spatio-temporal clusters (Fig. 4). Over a third of the occurrences (n = 60) belonged to catches between 1912 and 1924 in Panamá, collected in Panamá Bay, West Panamá, the Darién region, and the Taboga Islands. Another cluster in Panamá represents 15 occurrences between 1985 and 2015 from Chiriquí (n = 7), Coclé (n = 4), Darién (n = 2), and Veraguas (n = 2), most of which correspond to single records and accounts from fishers. In Colombia, the largest cluster contained 11 occurrences recorded between 2000 and 2010 in Utría National Park, the area with the highest number of occurrences in the northern Chocó (Fig. 4). All occurrences here were reported to be adult sawfishes by interviewees.

The current extent of occurrence of *P. pristis* in Panamá and Colombia ranged from 3009 to 13 958 km^2 and from 217 to 1025 km^2, respectively. The current extent corresponded to the spatio-temporal clusters mentioned above, hereafter referred to as bright spots. The extent of occurrence was 4.6 times larger for the 100 km home range compared to the 50 km home range for both countries (Table S5). A considerable reduction in the extent of occurrence for both countries was estimated at between 53 and 86% over the last 100 years (Table S5). Marine protected areas cover up to 21% (4393 km^2) of the historical extent of occurrence for Panamá, while for Colombia, only 3% (85 km^2) was protected. The area of sawfish occurrence that was protected before 2010 was 17% in Panamá and 3% in Colombia. For contemporary occurrences after 2010, these proportions increase to 28 and 8%, respectively.

4. DISCUSSION

In collating over a century of records of sawfish occurrences from Colombia and Panamá, results showed that sawfishes were historically distributed along the Pacific and Caribbean coastlines, but this distribution and their abundance appear to have decreased substantially with time. The paucity of recent observations and landings by fishers in most sampled areas aligns with the widely reported global decline of sawfishes (Faria et al. 2013, Dulvy et al. 2016).

In both countries, the majority of records were dated from the 20th century, with 79% of observations in Panamá and 69% in Colombia occurring before the year 2000. Historically, more biological expeditions took place in Panamá than on the Pacific coast of Colombia, most likely due to accessibility. Interview respondents stated that sawfish have never been commonly captured but noted the species has been particularly scarce for the last 20 yr. These results are consistent with recent research in the region, with the Colombian Red List of Endangered Species reporting that *Pristis pristis* populations are possibly extinct from the Colombian Caribbean (Gómez-Rodríguez et al. 2014) and have been absent from the Pacific coast since the last recorded capture in 2007 (Caldas et al. 2017). However, our results suggest the Darién region in Panamá and the northern Chocó region in Colombia are likely to retain local populations, since they are bright spots of sawfish occurrences within the last 10 yr. This is further supported by recent reports of sightings. In November 2020, an approximately 4 m sawfish was observed swimming in the mangrove forest of Coquí in the northern Chocó (O. Asprilla, nature guide from Coquí, pers. comm.). Moreover, continuing captures of *P. pristis* in gill nets throughout 2020 have been reported at Rompío, a locality near a turbid marine inlet of the Tuira River in Darién (Panamá). Here, the sawfish is called 'monã' in Emberá, the local Indigenous language, and is consumed by local people

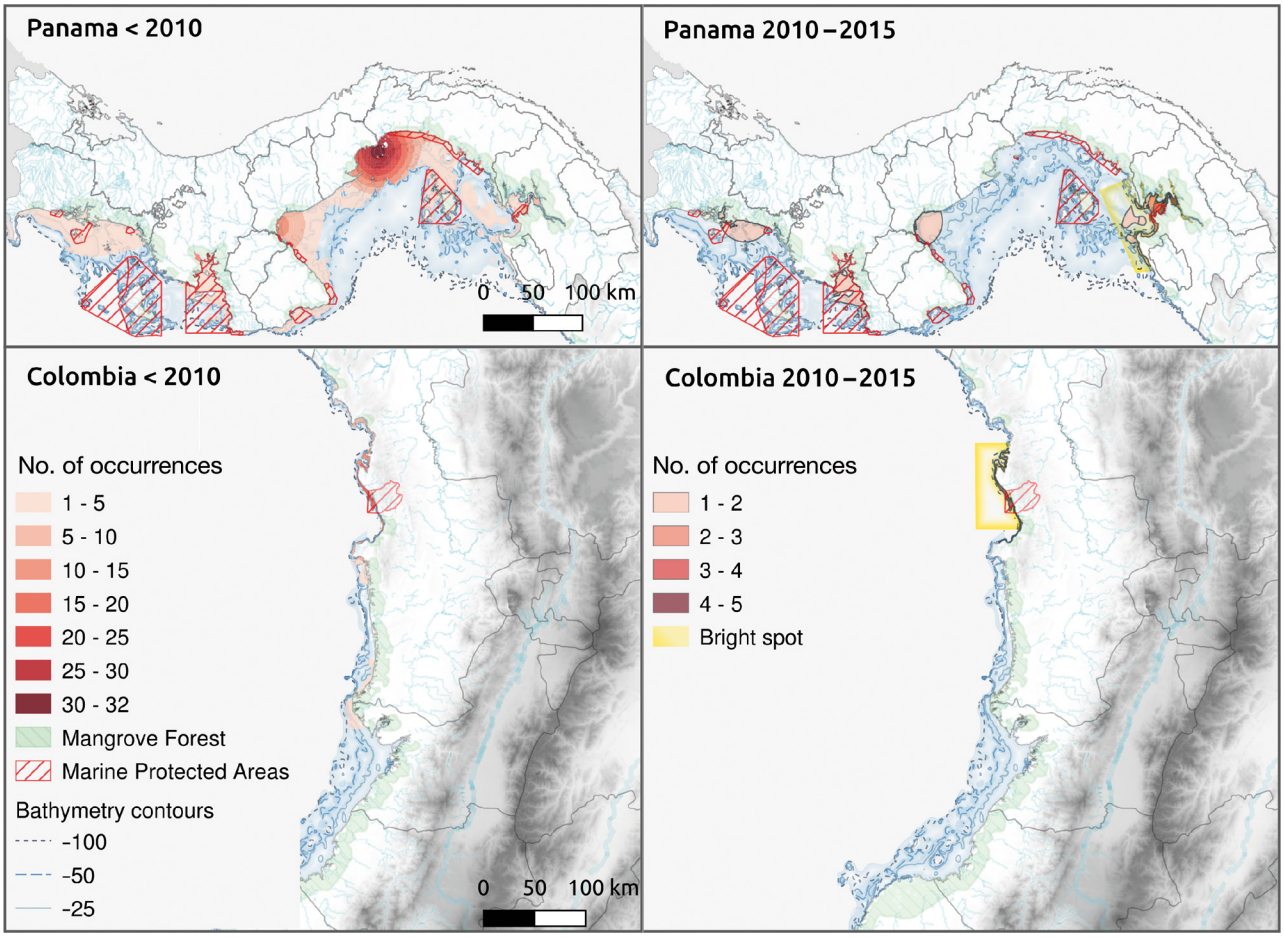

Fig. 4. Heat map of the probability distribution of largetooth sawfish *Pristis pristis* occurrences in Panamá and Colombia assuming a habitat range of 50 km and a maximum depth of 50 m. The colour gradient is a visualisation of the cumulative number of occurrences and not abundance. The left panels show occurrences prior to 2010, and the right show contemporary occurrences between 2010 and 2015. Bright spots are areas that potentially harbour extant populations of sawfish

(N. Senapi, native Emberá from Unión, Darién, pers. comm.).

Most contemporary occurrences (2010–2015) made up only 13% of the records from Colombia and 8% from Panamá. Approximately 40% of records were from expeditions in Panamá between 1912 and 1924, specifically from the Tuira River in Darién, the Taboga Islands, Panamá Bay, and West Panamá province (Meek & Hildebrand 1923, Breder 1927, Mitchell-Hedges 1928). These expeditions highlighted these areas as important sawfish pupping grounds, and the same locations overlap with local fisher knowledge from interviews and our spatial analysis. Fishers mentioned 2 main locations as important: in Panamá, the Darién region and the Bahía de Chame (La Chorrera region), and in Colombia, Utría National Park and the Golfo de Tribugá (Fig. 4). Utría National Park in the north of Colombia's Chocó department was responsible for 6 occurrences between 2000 and 2010. The northern Chocó is an area of particularly high biodiversity and is divided into 3 different management areas: 1 national park and 2 community-managed fishing areas. Locations highlighted in the interviews are characterised by high coverage of mangrove forests and low human population density. Recent studies in the eastern tropical Pacific region have also documented sawfish sightings between 2013 and 2018 in areas of dense protected mangrove forest, such as the Térraba-Sierpe National Wetlands in Costa Rica (Valerio-Vargas & Espinoza 2019) and the Tumbes region in northern Perú (Mendoza et al. 2017). These findings align with recent research that showed habitat availability, differential fishing pressure, and proximity to mangrove areas as factors strongly involved in sawfish residency, habitat suitability, and probability of local extinction (Yan et al. 2021).

4.1. Sawfish extent of occurrence

Sawfish travel extensive distances upstream in rivers of the region, as evidenced by records from sites located 30 km from the coast in Malambo and 600 km from the mouth of the Magdalena River (Table S2). Interview respondents noted that juvenile sawfish were generally found in river mouths and the shallow waters of small inland creeks, whereas adult sawfishes were also reportedly caught during deep-sea industrial trawling. This suggests that large sawfishes are not restricted to shallow and coastal areas and, similar to smalltooth sawfish (Simpfendorfer & Wiley 2005), may show mean size increases with depth and distance from the coast. In Florida, Poulakis & Seitz (2004) also reported that the majority of adult smalltooth sawfish encounters were in deep water on the seabed, overlapping with industrial trawl fishing grounds. This emphasises that data from trawl fisheries are important to understand the threats and potential strategies to halt sawfish extirpation. Furthermore, this also shows that conservation efforts cannot be entirely localised, and caution must be taken that coastal small-scale fishers are not vilified and further alienated in the fight to protect endangered marine species.

Our results suggest that there has been a considerable reduction in the extent of occurrence by as much as 86% in the last 100 yr. Yan et al. (2021) cite reduction in habitat availability, high fishing pressure, and distance to mangrove areas as key drivers of home range reductions of global sawfish populations. The bright spots we identified corroborate this theory, showing association with remote areas of high mangrove cover or proximity to marine protected areas. However, more research is needed to confirm if this is the case for the region overall. This may also be an artefact of the higher likelihood of reporting sawfish sightings in and around protected areas (due to increased awareness, enforcement, and reporting). The estimated area of extant populations for both countries falls well below the median required to ensure 5% occupancy of sawfish populations under several levels of fishing regimes as suggested by Yan et al. (2021). This implies that extant populations in small areas such as those found in northern Colombia are highly vulnerable to local extinction and highly dependent on connectivity to populations in Bajo Baudó (Colombia) and Darién (Panamá). Low dispersion of these populations would lead to isolation by distance and extirpation, as reported for other sawfish species (Yan et al. 2021).

4.2. Temporal shifts in sawfish size

The observed decline in total length of the largest observed sawfish individuals over the last century (Fig. 3a) is likely to be a result of a combination of increasing fishing pressure from offshore trawlers catching large adults, inshore gill nets catching adults during reproductive diadromy to and from rivers, and coastal habitat destruction. The paucity of data on sawfish restricts inference into any evolutionary changes in size structure through decreasing size at maturity. However, their inherent catchability and vulnerability to fisheries is very high (Dulvy et al. 2016), and for sharks, a decrease in size has been shown to have significant consequences for their vulnerability (Dulvy et al. 2003, Field et al. 2009) and rebound potential (Smith et al. 1998).

The overall decline in the frequency of sawfish sightings over time in the studied region was attributed primarily to mangrove deforestation and overfishing during the interviews. Respondents most frequently cited the increased use of gill nets as the reason for sawfish decline in shallow areas. Gill nets are pervasive in small-scale fisheries because they are cheap and effective and continue to provide economically viable catch rates at unsustainable levels of fishing effort (Northridge 1991). Fishers stated during interviews that sawfish were not directly targeted in gill net fisheries but rather were caught as by-catch and generally died before being released. Sawfish were not present in any of the artisanal fisheries data sets that we analysed for Panamá (Gulf of Montijo) and Colombia (northern Chocó, southern Pacific coast). Interview findings indicate that sawfish were never abundant or captured frequently by fishers, so the lack of records in fishery data sets may be a product of the intrinsic rarity of the species in addition to its widespread decline in the region. However, recent research in Bangladesh has shown that largetooth sawfish can persist in fishery landings despite global decline trends, primarily as incidental catch in gill nets (Hossain et al. 2015, Haque et al. 2020).

4.3. Sawfish and people

The strong historical association of coastal communities and mangroves in the Americas has shaped the use of mangrove resources (e.g. shells, tannins, charcoal, fish) since pre-Columbian times (López-Angarita et al. 2016), yet only since the emergence of gill nets as a common fishing gear in nearshore areas

would human–sawfish interactions have become more frequent. Elsewhere in the region, gill nets have been identified as a major threat to sawfish (Chasqui et al. 2017, Mendoza et al. 2017), and in areas heavily fished with this gear, there is evidence of the historical reduction of their populations, such as the Gulf of Nicoya in Costa Rica (Valerio-Vargas & Espinoza 2019). Interestingly, the database analysed for the northern Chocó region in Colombia includes data from a participatory monitoring program between 2010 and 2013, in an area that has restricted the use of nets since 2008 (Díaz & Galeano 2016). These regulations have been regarded as effective in terms of compliance by fishers (Díaz & Caro 2016) and the recovery of fisheries stocks in the area (López-Angarita et al. 2018a). In recent years, the Pacific coast of Colombia has seen a proliferation of small and often locally managed management zones with similar gear regulations (Castellanos-Galindo & Zapata Padilla 2019). As sawfish are mostly found entangled in gill nets, the reduction in the number of recent catches seen in Colombia could be a positive effect of the reduced number of nets being used in this area.

The use of sawfish for meat, medicine, and ornaments, among others, has been widely documented for several countries (McDavitt 2014, Leeney & Poncelet 2015, Leeney et al. 2018). Archaeozoological research in Panamá has shown sawfish were important for pre-Columbian cultures, not only as a source of food (Cooke & Jiménez 2008) but also for cultural and religious purposes and thus possessed a significance that transcended their practical usage (Cooke 2004a,b). Interviewees stated that once sawfish were caught, the meat was consumed, and the rostrum was cut off and kept mainly for decorative purposes or later sold to buyers looking for their teeth. In Panamá, some fishers reported that the teeth were fashioned into artificial spurs used in cockfighting, as documented from Perú (Cogorno Ventura 2001), something that has been observed by the authors on online sales sites and corroborated in other studies in Latin America (McDavitt 2014, Valerio-Vargas & Espinoza 2019). In Colombia, some fishers mentioned that the meat was used for consumption, but most pointed out that the rostrum was the most valuable sawfish body part because of its decorative value.

The eastern tropical Pacific has been highlighted in the agenda of sawfish global conservation because it has large, poorly studied regions with suitable sawfish habitat (Harrison & Dulvy 2014). Several fish workers stated that sawfishes were very frequent in the areas of Cuevita, Virudo, and Pizarro in the southern Chocó region of Bajo Baudó, but it was not possible to survey these sites as part of this study. The coverage of potentially suitable habitat for sawfishes in this area is considerably wider than in the northern Chocó region, with over 25 000 ha of estuaries and mangroves (Bernal et al. 2017). The area also includes the Baudó River delta, declared a Ramsar site in 2004 (Ramsar 2004). Historically, these areas were under substantial fishing pressure from industrial shrimp fisheries, suspended drift nets, and fixed gill nets, while lacking inclusive management zones for artisanal fishers (Velandia et al. 2019). However, with the prospect of reducing nearshore fishing pressure, community-based protected and management areas were established in 2017 in 2 mangrove areas (Frontera and El Encanto de los Manglares) (RUNAP 2018) resembling community fisheries management implemented in the northern Chocó region since 2008.

4.4. Conservation priorities

Future research efforts must focus on determining the status of any remnant sawfish populations in Bajo Baudó, especially since fisheries management legislation has been recently introduced. Another area of prime importance for future research is Sanquianga National Park in the southern Pacific of Colombia, an expansive area of suitable habitat for sawfish with relatively low human density, which could also represent an undetected bright spot. In countries with historically high levels of mangrove deforestation such as Colombia and Panamá (López-Angarita et al. 2016), management zones and protected areas have a crucial role in sawfish conservation, given that they not only may harbour the last functional populations of this Critically Endangered species but also could guarantee its long-term survival, acting as a shield against habitat degradation (López-Angarita et al. 2018b) and non-selective fishing practices (i.e. gill nets) (López-Angarita et al. 2018a). Further research should leverage eDNA as a novel non-invasive and rapid sampling technique to assess the presence of species (Simpfendorfer et al. 2016), especially in places where access and community surveys are restricted.

Remaining sawfish populations need critical management for sustained viability, yet without strong and urgent protection policy, populations will continue to decline. Moreover, implementation of the global strategy for sawfish conservation (Harrison & Dulvy 2014) will only be possible if interventions and regulations are established with local communities to

ensure local legitimacy, enforcement, and compliance (Rohe et al. 2017).

Our study contributes to other recent emerging research from the tropical eastern Pacific region in confirming the continuous distribution of the largetooth sawfish from Nicaragua to northern Perú (Mendoza et al. 2017, Valerio-Vargas & Espinoza 2019) and maps bright spots where more detailed and exhaustive surveys should be undertaken. Pushing sawfish onto national and regional conservation agendas is a priority, given the evidence that the species is still present in patches. However, actions must be put in place to overcome the gap between academic studies and their practical usability for conservation (O'Connell & White 2017). Even where sawfish are formerly protected under formal regulations such as in Bangladesh, the lack of awareness of the law by fishers and traders means sawfish are still being landed at relatively high rates (Haque et al. 2020). Therefore, in Colombia and Panamá, building an understanding of the cultural and socio-economic value of sawfish with local communities in the context of their livelihoods and resource should be the first step for the long-term conservation of this Critically Endangered species. The bright spots identified in this study allow for prioritisation of this work to areas of most urgent need but also to the geographical gaps in our knowledge of sawfish extent that require more targeted research.

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