

Richness distribution patterns of marine elasmobranchs in Colombia

Patrones de distribución de la riqueza de elasmobranquios marinos en Colombia

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Resumen. Se analizó la distribución de la riqueza de tiburones y batoideos marinos para el Caribe y el Pacífico colombiano. Se documentó un total de 138 especies en las aguas marinas cercanas a las costas de Colombia, incluidos 76 tiburones y 62 batoideos; 20 especies se encontraron en ambas costas y el Caribe presentó una mayor riqueza observada que el Pacífico. Los valores más altos de riqueza por unidad espacial se encontraron en el Pacífico, específicamente en las islas Gorgona y Malpelo. El Caribe presentó valores altos de riqueza tanto en la región insular como en la región norte. La completitud tuvo porcentajes más altos por unidad espacial en el Pacífico en comparación con el Caribe, y estuvo representada en su mayoría por valores menores al 90%. Esto último, sumado a que los estimadores de riqueza tuvieron valores mayores que la riqueza observada, indican que los inventarios y la descripción de la riqueza de tiburones y batoideos marinos en Colombia aún están incompletos. Pese a ello, los resultados de este estudio son relevantes para la toma de decisiones dirigidas a la conservación de este grupo taxonómico, tanto en áreas marinas protegidas como no protegidas del Pacífico y el Caribe colombiano.

Palabras clave: Rarefacción, completitud, coordenadas, batoideos, tiburones, neotrópico

Abstract. An analysis on the species richness distribution of marine sharks and batoids for the Colombian Caribbean and Pacific regions was carried out. A total of 138 species was documented in nearby marine waters off Colombia, including 76 sharks and 62 batoids; 20 species occurred on both coasts with the Caribbean generally having a higher observed richness than the Pacific. The Caribbean had high richness values both in the insular as well as in the northern region. However, the highest richness values per spatial unit in the Pacific islands of Gorgona and Malpelo, with completeness richness estimate represented mostly by values below 90%. Richness estimators showed values higher than the observed richness, indicating that the inventories and the description of marine shark and batoid richness in Colombia are still incomplete. Despite this, the results of this study are relevant to make decisions aimed at the conservation of this taxonomic group, both in marine protected and unprotected areas of the Pacific and Caribbean coasts of Colombia.

Key words: Rarefaction, completeness, coordinates, batoids, sharks, neotropics



INTRODUCTION

A global richness of more than 1,188 chondrichthyan species had been documented with 630 batoids and 509 sharks (Weigmann 2016). Studies on the distribution of chondrichthyan richness have identified Australia, Japan, Indonesia, South Africa, the central-western Atlantic, and Taiwan as biodiversity hotspots (Lucifora *et al.* 2011, Dulvy *et al.* 2014, Weigmann 2016). Weigmann (2016) reported elasmobranch richness in large marine regions totaling 216 species for the northwestern Atlantic, 151 for the northeastern Pacific, and 168 for the southeastern Pacific. For Colombian marine waters, Mejía-Falla & Navia (2019) documented 138 species with 76 sharks and 62 batoids species, placing Colombia as the third country with the highest elasmobranch richness in Latin America, after Mexico and Brazil.

Research on Chondrichthyans in Colombia has occurred since the early twentieth century, beginning with scientific studies carried out by Posada in 1909 (Acero 1988). However, only recently have studies focused on richness and biodiversity (Mejía-Falla *et al.* 2007, Navia *et al.* 2016, García 2017, Mejía-Falla & Navia 2019). Some studies have overestimated the richness of elasmobranchs in Colombia, including species whose natural latitudinal distribution range reduces the probability that they inhabit Colombian waters [(e.g., the white shark (*Carcharodon carcharias*) or the basking shark (*Cetorhinus maximus*) (Álvarez-León *et al.* 2013)]. On the other hand, there are generally few reports of deep-sea species, which leads to underestimate the species richness in the Caribbean Sea (García 2017). Recent studies have carried out significant taxonomic and systematic reclassifications of elasmobranchs (Castro 2011, del Moral-Flores *et al.* 2015, Acero *et al.* 2016, de Carvalho *et al.* 2016, Carpenter & De Angelis 2016, Last *et al.* 2016a, b, c; Naylor *et al.* 2016, Weigmann 2016, White & Naylor 2016), and Colombian species checklists (Mejía-Falla *et al.* 2007, 2011) had been recently updated (Mejía-Falla & Navia 2019). Despite this significant effort to update species occurrence records, little is known about the distribution of this group in Colombia.

Recent studies indicate that elasmobranchs are one of the most threatened vertebrate groups worldwide (Dulvy *et al.* 2014, Lauria *et al.* 2015, White *et al.* 2019), and this situation is not different in Colombia where more than 20% of these species are in some threat category (Chasqui *et al.*

2017). This is mainly due to high fishing pressures, by-catch, habitat degradation and pollution (Chasqui *et al.* 2017). However, biological, ecological and fishing knowledge of many elasmobranch species in Colombia is limited and their conservation status is uncertain.

The objective of this work was to identify richness distribution patterns of elasmobranchs in both the Caribbean Sea and the Pacific Ocean off Colombia to reveal potential richness hotspots. These results will allow to identify strategic areas and ecosystems, and species with high conservation value (Lucifora *et al.* 2011, 2012), as well as improving threat assessments under IUCN criteria and estimating the risk of extinction of marine elasmobranchs in Colombia.

MATERIALS AND METHODS

STUDY AREA

The study area included coastal and marine environments of the Caribbean Sea and Pacific Ocean of Colombia (IDEAM *et al.* 2007). The Caribbean Sea is located in the north and northwest of Colombia with a coastline of 1,932 km length and an area of 532,154 km². The Pacific is located in the western region of Colombia and has a coastline of 1,599 km length and a total area of 359,948 km² (CCO 2018)¹.

DATABASE

The checklist of elasmobranch species of Colombia is based on confirmed records from Mejía-Falla & Navia (2019). The occurrence data, based on longitude and latitude, are from two main sources: free access sources (secondary information) and projects developed in the country (primary information).

FREE ACCESS SOURCES

Records of occurrence available in the Global Biodiversity Information Facility (GBIF)² and the Marine Biodiversity Information System (SIBM)³ databases were used coupled with electronic catalogs and databases of national and international institutions and universities for our database (Table S1). Finally, occurrences in published catalogs of coastal fish from the Caribbean and the Tropical Eastern Pacific were also included (Robertson & Allen 2015, Robertson *et al.* 2015).

¹CCO. 2018. Gestión del territorio marino costero. Comisión Colombiana del Océano, Bogotá.
<<http://www.cco.gov.co/cco/areas/gestion-del-territorio-marino-costero.html>>

PROJECT DATA

Colleagues at various institutions in Colombia provided elasmobranchs occurrence data from the Caribbean and Pacific areas. Additionally, new species occurrences and range expansions were included from published literature (Nieto *et al.* 2003, Rubio *et al.* 2005, Navia *et al.* 2006, Grijalba-Bendeck & Acevedo 2009, Mejía-Falla & Navia 2009, Payán *et al.* 2010, Gámez-Barrera *et al.* 2012, Aceró *et al.* 2016, 2018; Anguila *et al.* 2016a, b). The taxonomy and systematics of each record used in our database, based on the Eschmeyer's Catalog of Fishes (Fricke *et al.* 2020), was verified and updated as necessary. Finally, all the data with satellite positioning information were submitted to a distribution filter to confirm they were within the limits of the study area.

DATA ANALYSIS

Two Excel files were built as input for species distribution analyzes: i) a "taxonomic" data sheet including class, order, family, genus and species categories for all specimens, and ii) a "position" data sheet with longitude, latitude and the taxonomic identity of each occurrence. Files were saved in .csv format and imported into the DataBase-Manager application of the ModestR analytical package (ModestR software - University of Vigo)⁴ (García-Roselló *et al.* 2013).

To generate the distribution maps and validate that each species was within the selected distribution ranges, species occurrence data were processed in the MapMaker application (ModestR), applying the alpha shape and the kernel density algorithms (Pelayo-Villamil *et al.* 2012). Once the species distribution maps were processed, results were exported as a file compatible with KnowBR to be analyzed with RWizard (Lobo *et al.* 2018).

Indices of richness and completeness (the number of species observed in comparison to those predicted as a percentage, indicating how well the richness is known in an area) were estimated using the KnowBR routine of the RWizard software (Lobo *et al.* 2018) to visualize the spatial distribution of richness and establish the appropriate spatial units sampled relative to the number of sharks and batoids in the country. Spatial units were considered as well-sampled when slope values were <0.02, completeness values were >90%, and a proportion of records per species were >15

(*i.e.*, the proportion between the number of records and the observed species). This routine is based on species accumulation curves that describe the relationship between the accumulated number of species and the replacement of the sampling effort (database records) to characterize the rate of increase with the sampling effort of each spatial unit. Thus, to determine if spatial units can be considered well-sampled, the slope of the species accumulation curve indicates the probability of finding a new species if sampling units continue to be added (Lobo *et al.* 2018).

For the visualization of the maps, a 15 x 15 min grid was selected using the following arguments: method= "incidence" (presence-absence data), cuts= 1 (threshold representing the proportion between the number of records in the samples and the number of species), and cut-off completeness= 1 (if the value of completeness is less than this threshold, the cell is considered non-informative) (García 2017, Lobo *et al.* 2018). This produced a total of 208 cells (128 in the Caribbean and 80 in the Pacific) since the surface of the Caribbean is larger than the Pacific.

Differences between observed and expected richness were evaluated using several estimators of the first and second order (Chao1, Chao2, ACE, ICE, and Jackknife) integrated in the EstimateS 9.1.0 software package (Colwell 2013). The following arguments were used: 100 randomizations and cut-off point= 10 for ACE, ICE and shared species. The respective rarefaction curves with their estimators were generated for global richness and richness per region. These estimators are non-parametric models that may estimate species richness either for abundance (Chao 1) or incidence (Chao 2) data (Chao & Chiu 2016). For abundance data (Chao 1) it is important to consider the rare species that are represented by one (singletons), two (doubletons) or by a few individuals, whereas for incidence data (Chao 2) it is important to consider the infrequent species that are present in one (uniques), two (duplicates) or in a few replicate samples (Gotelli & Colwell 2011, Chao & Chiu 2016). For ACE (Abundance-based Coverage Estimator) and ICE (Incidence-based Coverage Estimator), the cut-off point values indicate the number of rare and infrequent species, respectively, taken into account in the richness estimation; that is because the abundant and frequent species do not carry information about undetected species (Chao & Chiu 2016).

²GBIF. 2020. Global Biodiversity Information Facility. <<https://www.gbif.org>>

³SIBM. 2020. Sistema de Información Sobre Biodiversidad Marina. <<https://siam.invemar.org.co/sibm>>

⁴Modest R, Software for species distribution data management, University of Vigo. <<http://www.ipez.es/modestr>>

The similarity in the composition of the elasmobranch richness between the Pacific and the Caribbean coasts was assessed by applying the shared richness estimator (Chao-Shared) and the richness-based similarity indices (Jaccard and Sørensen). All analyses were performed with SpadeR (Chao *et al.* 2015). The Sørensen estimator (C_{qN}) indicates the estimated average proportion of the shared species between the two regions; the Jaccard estimator (U_{qN}) indicates the estimated proportion of the shared species (this is a value equivalent to the percentage of shared species compared to the total number of species) (Chao *et al.* 2015). The complementary measurement of the non-shared species proportion is obtained by: $1 - C_{qN}$ or $1 - U_{qN}$ where 0 indicates that the two regions are identical, and 1 indicates that they are entirely different (Chao *et al.* 2015). The value was obtained by computing the total relative abundances of the species shared between the two regions (Chao *et al.* 2015).

RESULTS

A total of 12,996 records belonging to the 138 species of marine sharks (75) and batoids (60) confirmed to Colombia were collected in 2,125 locations. Geopositioned records of 66 species were identified in the Pacific Ocean (36 sharks and 31 batoids) and 91 in the Caribbean Sea (55 sharks and 33 batoids). These species were grouped into 33 families (18 sharks and 15 batoids) with Carcharhinidae contributing most to shark diversity in Colombia (14.49%), followed by Scyliorhinidae (8.70%), Etmopteridae (6.52%), Sphyrnidae, and Triakidae (5.07% each) (Fig. 1). For batoids, Rajidae was the family with the highest contribution to the richness of this group (9.42%), followed by Narcinidae and Urotrygonidae (5.80% each) (Fig. 1). Eleven shark families and 11 batoid families occurred in both regions; five shark families were exclusive to the Caribbean and only one to the Pacific, whereas for batoids, two families were exclusive to the Pacific and two more to the Caribbean (Table 1; Fig. 1).

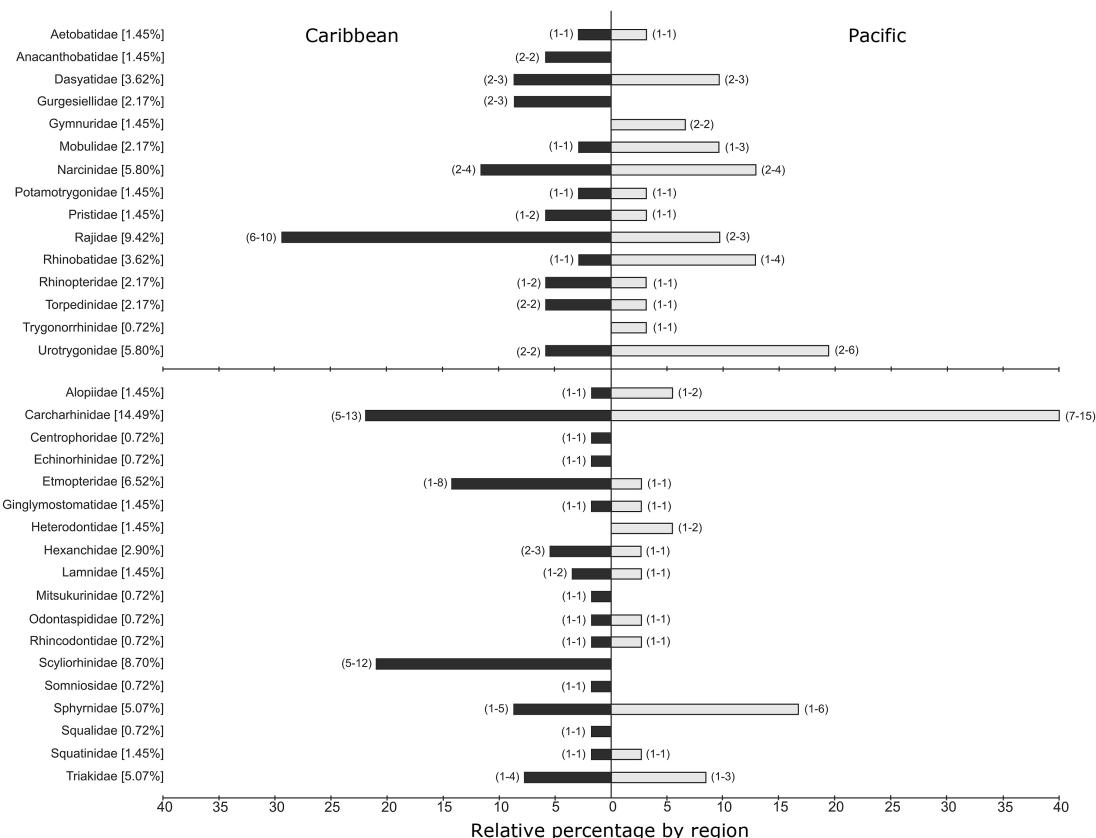


Figure 1. Relative contribution of each family to the total richness of marine elasmobranchs in Colombia (values in brackets). The values in parentheses correspond to the total number of genus (first value) and species (second value) per family / Contribución relativa de cada familia a la riqueza total de elasmobranquios marinos en Colombia (valores entre paréntesis). Los valores entre paréntesis corresponden al número total de géneros (primer valor) y especies (segundo valor) por familia

Table 1. Families and species of marine sharks and batoids recorded in Colombia (Pacific Ocean and Caribbean Sea) and those shared by the two regions / Familias y especies de tiburones y batoideos marinos registrados en Colombia (océano Pacífico y mar Caribe), y aquellas compartidas entre las dos regiones

Sharks			Batoids		
Shared	Only Caribbean	Only Pacific	Shared	Only Caribbean	Only Pacific
Alopiidae <i>Alopias superciliosus</i>		<i>Alopias pelagicus</i>			
Carcharhinidae <i>Carcharhinus altimus</i> <i>Carcharhinus falciformis</i> <i>Carcharhinus leucas</i> <i>Carcharhinus limbatus</i> <i>Carcharhinus longimanus</i> <i>Galeocerdo cuvier</i> <i>Negaprion brevirostris</i> <i>Priacanthus glauca</i>	<i>Carcharhinus acronotus</i> <i>Carcharhinus perezii</i> <i>Carcharhinus porosus</i> <i>Rhizoprionodon lalandii</i> <i>Rhizoprionodon porosus</i>	<i>Carcharhinus albimarginatus</i> <i>Carcharhinus brachyurus</i> <i>Carcharhinus cerdale</i> <i>Carcharhinus galapagensis</i> <i>Nasolamia velox</i> <i>Rhizoprionodon longurio</i> <i>Triaenodon obesus</i>		<i>Aetobatus narinari</i>	<i>Aetobatus laticeps</i>
Centrophoridae	<i>Centrophorus granulosus</i>			<i>Schroederobatis americana</i>	<i>Springeria longirostris</i>
Echinorhinidae	<i>Echinorhinus brucus</i>			Dasyatidae <i>Pteroplatygon violacea</i>	<i>Hypanus americanus</i>
Etmopteridae	<i>Etmopterus bullisi</i> <i>Etmopterus carteri</i> <i>Etmopterus gracilispinis</i> <i>Etmopterus hilianus</i> <i>Etmopterus perryi</i> <i>Etmopterus robinsi</i> <i>Etmopterus schultzi</i> <i>Etmopterus virens</i>			<i>Hypanus guttatus</i>	<i>Hypanus dipterurus</i> <i>Hypanus longus</i>
Ginglymostomatidae	<i>Ginglymostoma cirratum</i>	<i>Ginglymostoma unami</i>		Gurgesiellidae <i>Cruriraja poeyi</i> <i>Cruriraja rugosa</i> <i>Gurgesiella atlantica</i> <i>Fenestraja plutonia</i> <i>Fenestraja sinusmexicanus</i>	
Heterodontidae		<i>Heterodontus francisci</i> <i>Heterodontus mexicanus</i>			
Hexanchidae <i>Hexanchus griseus</i>	<i>Heptanchias perlo</i> <i>Hexanchus nakamurai</i>	<i>Notorynchus cepedianus</i>		Gymnuridae <i>Gymnura crebipunctata</i> <i>Gymnura marmorata</i>	
Lamnidae <i>Isurus oxyrinchus</i>	<i>Isurus paucus</i>			Mobulidae <i>Mobula birostris</i>	<i>Mobula munkiana</i>
Mitsukurinidae	<i>Mitsukurina owstoni</i>				<i>Mobula thurstoni</i>
Odontaspidae		<i>Odontaspis ferox</i>		Narcinidae <i>Diplobatis colombiensis</i> <i>Diplobatis guamachensis</i> <i>Diplobatis picta</i> <i>Narcine bancroftii</i>	<i>Diplobatis ommata</i> <i>Narcine entemedor</i> <i>Narcine leoparda</i>
Rhincodontidae <i>Rhincodon typus</i>				Potamotrygonidae <i>Styracura schmardae</i>	<i>Styracura pacifica</i>
Scyliorhinidae	<i>Apristurus caninus</i> <i>Apristurus parvipinnis</i> <i>Apristurus riveri</i> <i>Galeus arai</i> <i>Galeus cadenati</i> <i>Schroederichthys maculatus</i> <i>Scyliorhinus boa</i> <i>Scyliorhinus haekelii</i> <i>Scyliorhinus hesperius</i> <i>Scyliorhinus retifer</i> <i>Scyliorhinus torrei</i>	<i>Cephalurus cephalus</i>		Pristidae <i>Pristis pectinata</i>	<i>Pristis pristis</i>
Somniidae	<i>Somnioides spp.</i>			Rajidae <i>Breviraja nigrovittalis</i> <i>Breviraja spinosa</i> <i>Dactylobatus clarkii</i> <i>Dipturus bullisi</i> <i>Dipturus garricki</i> <i>Dipturus teevani</i> <i>Rajella fuliginosa</i> <i>Rostroraja cervigoni</i>	<i>Rajella nigerrima</i> <i>Rostroraja equatorialis</i> <i>Rostroraja velezi</i>
Sphyrnidae <i>Sphyrna lewini</i> <i>Sphyrna media</i> <i>Sphyrna mokarran</i> <i>Sphyrna tiburo</i>	<i>Sphyrna tudes</i>	<i>Sphyrna corona</i> <i>Sphyrna zygaena</i>		Rhinobatidae <i>Pseudobatos percellens</i>	<i>Pseudobatos glaucoptigma</i> <i>Pseudobatos leucorhynchus</i> <i>Pseudobatos planiceps</i> <i>Pseudobatos prahli</i>
Squalidae	<i>Squalus cubensis</i>			Rhinopteridae <i>Rhinoptera bonasus</i> <i>Rhinoptera brasiliensis</i>	<i>Rhinoptera steindachneri</i>
Squatinaidae	<i>Squatina david</i>	<i>Squatina armata</i>		Torpedinidae <i>Tetronarce nobiliana</i>	<i>Tetronarce tremens</i>
Triakidae	<i>Mustelus canis</i> <i>Mustelus highmani</i> <i>Mustelus minicanis</i> <i>Mustelus norrisi</i>	<i>Mustelus dorsalis</i> <i>Mustelus henlei</i> <i>Mustelus lunulatus</i>		Trygonorrhinidae <i>Urotrygon jamaicensis</i> <i>Urotrygon venezuelae</i>	<i>Zapteryx xyster</i>
16 species	39 species	20 species	3 species	30 species	27 species

The family that contributed most to shark richness in the Caribbean was Carcharhinidae (22.80%), followed by Scyliorhinidae (21.67%) and Etmopteridae (14.03%). Similarly, the family that contributed most to shark richness in the Pacific was Carcharhinidae (42.85%), followed by Sphyrnidae (17.14%) and Triakidae (8.57%) (Fig. 1). For batoids, the families with the highest richness in the Caribbean were Rajidae (29.41%) and Narcinidae (11.76%), followed by Dasyatidae and Gurgesiellidae (8.82% each). In the Pacific, Urotrygonidae (19.35%), Narcinidae and Rhinobatidae (12.90% each) contributed most to species richness (Fig. 1). Considering all elasmobranchs, the families with higher richness in the Caribbean were Carcharhinidae (5 genera, 13 species) and Rajidae (6 genera, 10 species) respectively, meanwhile in the Pacific were Carcharhinidae (7 genera, 15 species) and Urotrygonidae (2 genera, 6 species) (Fig. 1). Comparatively, the Caribbean showed a higher richness of sharks than the Pacific, with 55 and 36 species respectively, whereas the batoids richness in the two areas was more homogeneous, 33 species in the Caribbean and 30 in the Pacific (Table 1).

The most significant number of elasmobranch records was obtained in the Pacific Ocean, specifically in the Gorgona and Malpelo Islands; these were the spatial units with the highest number of reports at the country level (> 700 each; Fig. 2a). In the Pacific, areas such as Marzo Cape, Corrientes Cape, Tortugas Gulf and Malaga Bay were also highlighted. In the Caribbean, the insular areas of San Andres and Providencia (≈ 500 records) were highlighted, followed by Serrana, Serranilla, and Bajo Nuevo cays; in the continental shelf, the number of records per spatial unit was more homogeneous, highlighting the Gulf of Salamanca and Fuerte Island (Fig. 2a).

The highest number of elasmobranch species per spatial unit was found in the Pacific, especially in the Gorgona and Malpelo Islands with 47 and 37 species, respectively (Fig. 2b). In the coastal zone, the spatial units corresponding to the Tortugas Gulf, Guapi Cove and Tribuga Gulf showed richness between 15 and 30 species. In the Caribbean, insular spatial units as San Andres, Providencia and Serrana Cay (~ 15 to 25 species), and coastal spatial units as the coasts of Barranquilla, Santa Marta, Palomino, and Riohacha, with similar values to the insular units, were highlighted (Fig. 2b).

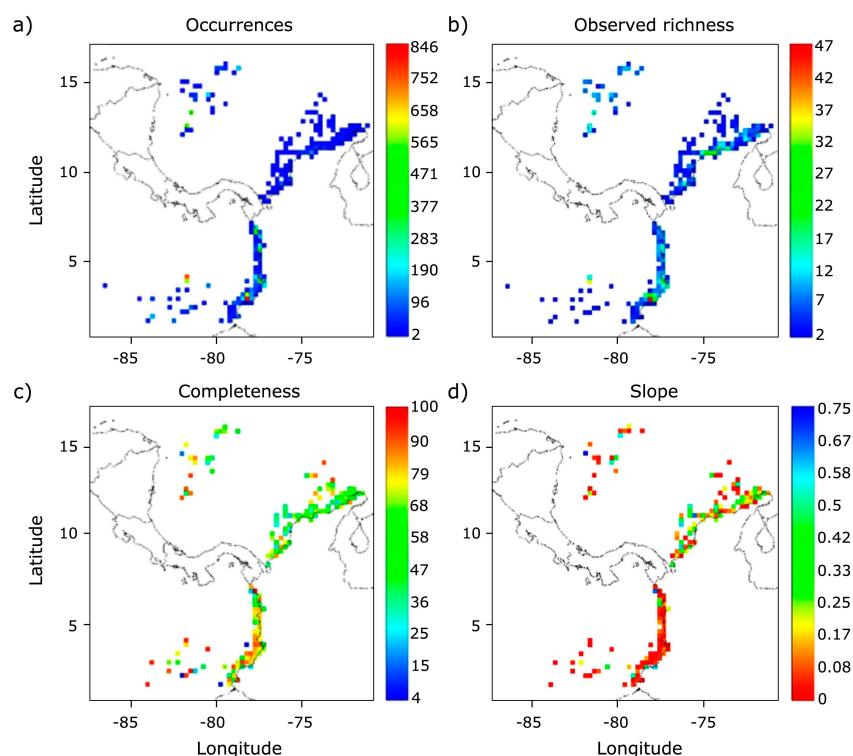


Figure 2. Distribution of the occurrence (a), richness (b), completeness (c) and spatial estimation of the slope of the accumulation curve of shark and batoid species (d) in the Colombian Pacific and Caribbean regions. The heat scale per cell represents (a) the number of records, (b) the number of species, (c) percentage of completeness and (d) the value of the slope, where values close to 0 (zero) indicates proximity to asymptotic richness / Distribución de la ocurrencia (a), riqueza (b), completitud (c) y estimación espacial de la pendiente de la curva de acumulación de especies de tiburones y batoideos (d) en las regiones del Pacífico y el Caribe colombianos. La escala de calor por celda representa (a) el número de registros, (b) el número de especies, (c) porcentaje de completitud y (d) el valor de la pendiente, donde los valores cercanos a 0 (cero) indican proximidad a la asintota

The highest percentages of completeness reached in the Pacific region was found in seven ocean units and two coastal units (Gorgona Island and Arusi) with values equal to or higher than 90% (Fig. 2c). The Caribbean showed fewer spatial units with high completeness values, being these located mainly in oceanic and insular zones. Coastal areas as Riohacha, Arboletes, Fuerte Island and San Bernardo Island showed completeness values between 70 and 90% (Fig. 2c).

The slopes of the species accumulation curves by spatial units showed the lowest (\approx asymptotic) values for the Pacific, both in the oceanic and coastal areas, indicating that the observed richness was closer to the predicted richness on this region compared to the Caribbean (Fig. 2d). The general rarefaction curve had an asymptotic tendency (slope= 0.031), with an observed richness of 138 species, lower than all calculated estimators and close to some of them (*i.e.*, Chao1= 140 and ACE= 141). All estimators were relatively close, varying between 140 (Chao1) and 158 species (second-order Jackknife), and whose confidence intervals were within the range of the maximum number of species that would

Table 2. Comparison of the results of the estimators (n) and the respective slopes (m) of the rarefaction curves for each region (Pacific and Caribbean) / Comparación de los resultados de los estimadores (n) y las respectivas pendientes (m) de las curvas de rarefacción para cada región (Pacífico y Caribe)

Estimators	n Pacific	m	n Caribbean	m
Chao1	68	0.0165	92	0.0352
Chao2	69	0.0150	100	0.0392
ACE	69	0.0158	94	0.0334
ICE	69	0.0136	99	0.0317
1º Jackknife	72	0.0179	104	0.0430
2º Jackknife	72	0.0117	109	0.0394

be expected (according to the literature) and confirmed for Colombia (Fig. 3A). The predicted richness for the Pacific and Caribbean regions was higher than the observed, and the results of the rarefaction curve and its estimators (predicted richness) indicate that in the Caribbean region there is a higher number of species (Table 2; Fig. 3B).

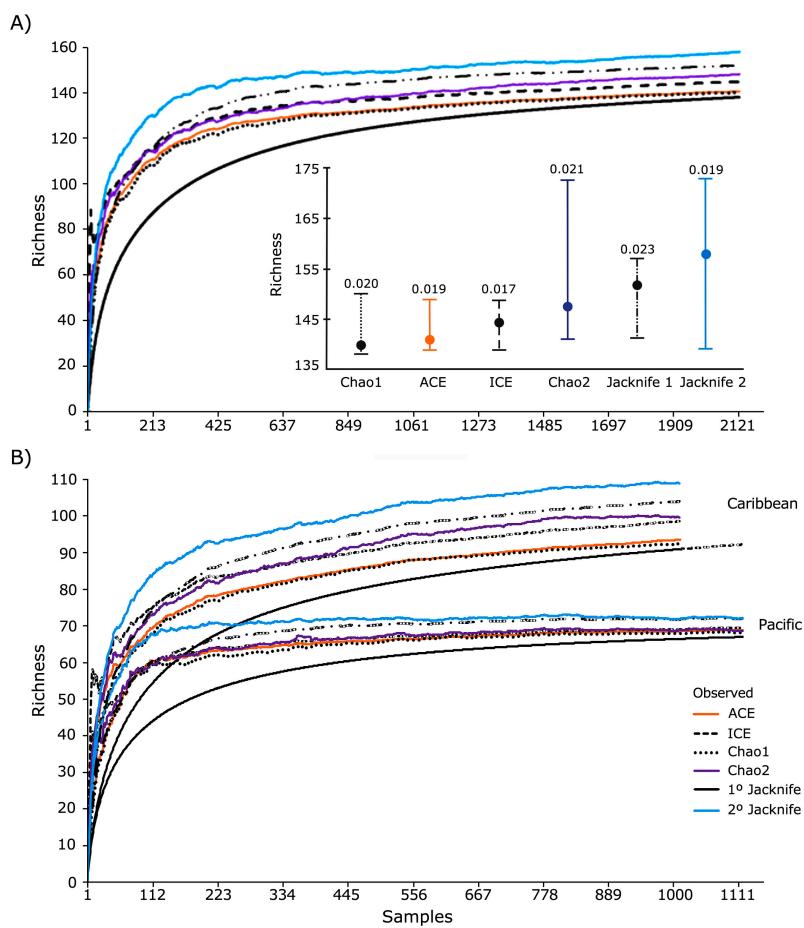


Figure 3. Species accumulation curves of marine sharks and batoids in Colombia with their respective estimators. A) For both regions; graph inside shows the comparison of the estimators regarding their accuracy in the measurement of asymptotic richness in Colombia; the value above the estimators corresponds to the slope of the curve. B) For each region, Caribbean (above) and Pacific (below) / Curvas de acumulación de especies de tiburones y batoideos marinos en Colombia, con sus respectivos estimadores. A) Para ambas regiones; el gráfico interior muestra la comparación de los estimadores con respecto a su precisión en la medición de la riqueza asintótica en Colombia; El valor sobre los estimadores corresponde a la pendiente de la curva. B) Para cada región, Caribe (arriba) y Pacífico (abajo), por separado

The shared richness estimator (Chao-Shared= 21, CI= 18-26) was very close to the observed value (20 species), indicating that there may be a few shared species, but that they have not yet been registered in any of these regions. The species richness similarity indices between regions (Jaccard= 0.145 and Sørensen= 0.253) showed that the Pacific and the Caribbean share a assemblage of species that would not represent more than 25% of the total number of species, and therefore, that these two geographical regions have a high difference in species composition (Jaccard $1-U_{qN}$ = 0.855; Sørensen $1-C_{qN}$ = 0.747).

DISCUSSION

Although studies related to the elasmobranch richness in Colombia have increased in recent years (Mejía-Falla *et al.* 2007, 2011), and despite being considered the third country with the highest richness of these species in Latin America (Mejía-Falla & Navia 2019), knowledge about the distribution of their richness is limited. García (2017) studied the patterns of richness distribution of demersal elasmobranchs on the Caribbean coast, whereas Navia *et al.* (2016) presented a zoogeographic study of the elasmobranchs of Colombia. However, this is the first study that analyzes the spatial distribution of the marine elasmobranch richness, including both coasts, and therefore, it becomes an important input for the establishment of marine areas of importance for the conservation of these species in Colombia.

The Caribbean showed a higher observed richness than the Pacific probably because it has more total area and a longer coastline. Carrillo-Briceño *et al.* (2018) quantified that for all the provinces in the Western Atlantic and Eastern Pacific, which surround Colombia, there is a positive correlation between the total area of the provinces and coastal length with the species diversity. This is likely related to larger area coverage by numerous habitats and ecosystems, leading to a higher marine elasmobranch diversity (Briceño *et al.* 2018).

Based on the estimators of the accumulation curves and their confidence intervals, our results indicate that species richness of sharks and batoids in Colombia could increase between 12 and 20%, reaching a value between 158 and 173 species. Thus, it is still necessary to enhance sampling in areas with little or no information since in this study records were verified in only 17% of the Colombian jurisdictional marine waters. Furthermore, the distribution of the records was similar between the Caribbean and the Pacific, with high values in the coastal spatial units and very few in oceanic waters, except for the San Andres and Providencia Archipelago and Malpelo Island.

The highest richness observed in the coastal quadrants could be related both to the sources of information available (fisheries studies, scientific cruises, and recreational diving), and to the higher number of studies carried out in these marine areas. For the Pacific region, Mejía-Falla & Navia (2017) found that out of 500 studies related to marine fisheries, a high percentage were carried out in the influence areas of the Gorgona and Malpelo Islands, as well as in the Buenaventura Bay and the north of Choco. On the other hand, for the insular Caribbean region, the records were concentrated around the San Andres and Providencia Islands, which have a significant diving activity (Navia & Mejía-Falla 2015). In contrast, in the northern cays, the records came mainly from fishing vessels, which directed their effort towards shark capture, but data only was available until 2009 when the fishery ended (Castro-González & Ballesteros-Galvis 2009). The distribution of information in the continental Caribbean was similar, with records concentrated in areas of high tourist activity such as Taganga and the Rosario Islands, or areas of high fishing activities as Bocas de Ceniza, Tasajera, and Guajira, among others (Caldas *et al.* 2009).

Species that have not yet been documented in Colombian waters are expected to be related to environments that have not yet been explored from scientific research or that have difficulties in implementing monitoring, such as oceanic and/or deep water ecosystems (> 200 m). For example, the Caribbean region, where more deep-sea research cruises have been carried out, showed a significantly higher number of elasmobranch species in these ecosystems.

Precisely, the high number of deep-sea species recorded in the Caribbean highlighted the difference in richness between the two regions. This result could also be due to the fact that the Colombian Caribbean belongs to the Greater Caribbean biogeographic region, which has been identified as a elasmobranch global hotspot (Weigmann 2016) and one of the important areas of cartilaginous fish endemism (Musick *et al.* 2004).

The richness identified for the Pacific was lower than for the Caribbean in our study, and it is also lower than in neighboring countries such Ecuador, Peru and Costa Rica (Martínez-Ortiz & García-Domingo 2013, Cornejo *et al.* 2015, Espinoza *et al.* 2018). Robertson & Allen (2015) proposed that the low diversity of elasmobranchs in the Eastern Tropical Pacific is due to the small number of coastal habitats (mainly continental) compared to the greater geographical complexity of the Caribbean, with a wider continental shelf and more oceanic islands.

The detailed analysis of the spatial units from the marine area of the Gorgona National Natural Park showed the highest richness in the entire country (> 40 species). This result places it as one of the richest areas in elasmobranchs in the Eastern Pacific region (from Alaska to Chile) and being only surpassed or equaled by some locations in the Gulf of California (Navia, unpubl. data). Thus, preserving integrity of this marine protected area will contribute to the conservation of almost 50% of the elasmobranch species recorded in the Colombian Pacific. Similarly, the second location in terms of richness in the Pacific is the Malpelo flora and fauna sanctuary, an oceanic island dominated by pelagic, oceanic and migratory species. Although Gorgona and Malpelo Islands are marine protected areas, it is important to strengthen community fishery agreements for the use of the Gorgona buffer zones, as well as control and surveillance actions against illegal fishing in both marine protected areas.

The insular region of the Caribbean had a moderately high richness, mainly influenced by oceanic, pelagic shark species, and a significant number of deep-sea species. This result is directly related to the characteristics of the San Andres Archipelago, where almost all the records were obtained around the islands or cays, mainly from places that would function as aggregators of species, structure providing shelter, food, or rest, and places associated with nursery areas. Therefore, the emerged areas of the Archipelago must be considered as priority areas for the conservation of pelagic species. However, the critical involvement of deep-sea species in this region should also be considered, and thus, maintain a strict control over the pressures that affect these species. This is especially true because these species are considered even more vulnerable than large sharks with slow life history (Dulvy *et al.* 2014).

Despite the high marine elasmobranch richness of Colombia, the shared species between the two regions is relatively low and mainly composed by large sharks and batoid species with high vagility. This low value was related to the vicariance events associated with the emergence of the Isthmus of Panama (Navia *et al.* 2016). This gave rise to speciation, diversification, and extinction processes due to the generation of differentiated environmental conditions between the two regions (Carrillo-Briceño *et al.* 2018), and that led to only large body-sized species being able to overcome the imposed barriers. This result is supported by the fact that the shared species are mostly sharks of the genus *Carcharhinus*, while the typical fauna of each coast was associated with small species as those of the Etmopteridae and Scyliorhinidae families for the Caribbean, and Urotrygonidae and Rhinobatidae families for the Pacific Ocean.

The overall results of this study indicate that the estimation of the elasmobranch richness and its distribution in Colombia, although incomplete, corresponds to robust information that contributes to the conservation of these species, both in marine protected and unprotected areas of the Pacific and Caribbean of Colombia, where many of them are considered threatened in the IUCN Red List and in the Colombian marine fish red book (Dulvy *et al.* 2014, Chasqui *et al.* 2017).

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SUPPLEMENTARY MATERIAL

table S1. List and abbreviation of the national and international institutions and universities reviewed in this work to obtain occurrence records from their electronic catalogs and databases / Lista y abreviatura de las instituciones y universidades nacionales e internacionales revisadas en este trabajo para obtener registros de ocurrencia a partir de sus catálogos electrónicos y bases de datos

National	International
UNSSA - Universidad Nacional Sede San Andrés (San Andrés)	AfroBIS - Iziko South African Museum, Shark Collection (South Africa)
PNNG - Colección Biológica Marina de Referencia de la Estación Biológica "Henry von Praeli" Parque Nacional Natural Gorgona (Isla Gorgona)	AMNH - American Museum of Natural History (Washington)
ICN-MHN - Instituto de Ciencias Naturales de la Universidad Nacional de Colombia (Bogotá)	CAS - California Academy of Sciences (San Francisco)
INV PEC - Museo de Historia Natural Marina de Colombia - MHNMC - Sección Peces (Santa Marta)	FLMNH - Florida Museum of Natural History (Gainesville)
	GCRL - Gulf Center Research Laboratory (Ocean Springs, USA)
	MCZ - Museum of Comparative Zoology, Harvard University, Cambridge (Massachusetts)
	MNHN - Muséum National histories Naturelle (Paris)
	NRM - Swedish Museum of Natural History (Sweden)
	SIO - Scripps Institution of Oceanography, University of California (San Diego)
	TCWC - Texas A&M University, Cooperative Wildlife Collection (Texas)
	USNM - National Museum of Natural History (Washington)