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## ARTÍCULO DE INVESTIGACIÓN / RESEARCH ARTICLE

**SPATIAL RICHNESS PATTERNS OF SOFT-BOTTOM FISH IN THE COLOMBIAN CARIBBEAN CONTINENTAL SHELF AND SLOPE****Patrones de distribución espacial de la riqueza de peces de fondos blandos en la plataforma y talud continentales del Caribe Colombiano**

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**ABSTRACT**

This study presents a spatial analysis of species richness of soft-bottom bony and cartilaginous fish species in the Colombian Caribbean. The dataset consisted of 625 species distributed among 15651 georeferenced occurrences. The global richness completeness analysis suggests that the list is close to completion but that probably more species await being registered at greater depths. In spatial terms, our knowledge of fish richness remains incomplete as none of the spatial units, in which the general area was divided reached 100 % completeness and few reached 70 % or higher completeness probably due to the incidence of numerous rare species. The Guajira, Palomino, Tayrona and Golfo de Salamanca zones, displayed the highest observed and predicted richness. The Galerazamba, Arco (coralline archipelago) and Arboletes zones were predicted to have high species richness. In view of the results, marine protected areas need to be expanded to include soft-bottom habitats. Future research efforts should focus on the high species richness areas observed and predicted and surveys should include more extensively depth locations.

**Keywords:** biodiversity, Colombian Caribbean, demersal fish, mapping.

**RESUMEN**

Este estudio presenta un análisis espacial de la riqueza de especies de peces óseos y cartilaginosos de fondos blandos del Caribe Colombiano. El conjunto de datos consiste de 625 especies distribuidas en 15651 registros georeferenciados. El análisis de completitud global de riqueza sugiere que la lista está próxima a estar completa pero que probablemente mas especies están pendientes de ser registradas a mayores profundidades. En términos espaciales el conocimiento de la riqueza de especies se mantiene incompleto ya que ninguna de las unidades espaciales en que el área general fue dividida, alcanzo el 100 % de completitud y pocas alcanzaron el 70 % o mas, probablemente debido a la influencia de muchas especies raras. Las zonas Guajira, Palomino, Tayrona y el Golfo de Salamanca mostraron la mayor riqueza observada y esperada. Para las zonas Galerazamba, Arco (archipiélago coralino) y Arboletes se predice alta riqueza de especies. En vista de los resultados, las áreas marinas protegidas deben expandirse para incluir hábitats de fondos blandos. Esfuerzos futuros de investigación deben enfocarse en las áreas de alta riqueza de especies tanto observada como esperada e incluir más extensamente localidades profundas.

**Palabras clave:** Caribe Colombiano, fondos blandos, peces, mapeo, riqueza.

## INTRODUCTION

Accurate knowledge of the species present in a particular area or region are condition *sine qua non* for informed management, be it in terms of conservation (restauration, protected areas), exploitation (fisheries, tourism) or as input for basic science disciplines including biogeography or macroecology. Species lists are, however, of limited utility. What makes them operational is the study of the distribution patterns in time and space of the species in the list.

In a recent study, García and Armenteras (2015) produced an atlas of the soft-bottom demersal fish species (both bony and cartilaginous) of the Colombian Caribbean Sea (discussed below). The georeferenced occurrences (latitude and longitude) of each species are depicted in the corresponding map. This information has provided the opportunity for studying the joined spatial distribution of the species in the atlas, i.e., the distribution pattern of species richness in space.

The taxonomic knowledge gained from studies that have described the demersal soft-bottom fish fauna of the Colombian Caribbean Sea is fairly advanced, although rather scattered, some examples of which include Acero and Garzón-Ferreira (1995), Garrido-Linares and Acero (2006), Mejía-Falla *et al.* (2007) and Roa-Varón *et al.* (2007). However, although general distribution of these species has come from expert opinion, no quantitative work (georeferenced occurrences) has mapped the presence of soft-bottom fish species in the Colombian Caribbean, except García and Armenteras (2015). In general, quantitative mapping of the distribution of marine species in Colombia is a new endeavor, and it is even more novel to map the species richness.

This work presents and discusses maps of the (1) observed soft-bottom fish species richness (bony and cartilaginous fishes), (2) estimates of asymptotic (predicted) richness and (3) estimates of completeness of inventories in a number of spatial units or cells along the Caribbean coast of Colombia. Knowledge of the observed and predicted spatial distribution of species richness may assist in proposals for directing the informed establishment of marine protected areas (MPAs)

beyond simple aesthetic considerations, and as a guide for future fieldwork focused on spatial units incompletely surveyed for species.

## MATERIALS AND METHODS

The georeferenced occurrences of soft-bottom fishes come mainly from García and Armenteras (2015, their Table 1) who covered the time period from 1964 to 2010, a depth range from 0 to 1800 m and spans the complete latitude gradient corresponding to the Colombian Caribbean Sea continental shelf and slope. Additional occurrences were obtained from the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org>). The GBIF data were imported using the free software ModestR (García-Roselló *et al.*, 2013) and filtered to exclude occurrences outside the Colombian Caribbean in addition to those in the archipelago San Andrés and Providencia. Both sources were crosschecked to avoid duplication of data.

Spatial analysis of richness and completeness (percentage representing the observed versus predicted number of species) were conducted using the KnobR application of the free software RWizard that is an open-source interface designed to facilitate the interaction with R statistical software (R Core Team, 2015), while KnobR is an R application specifically designed to work in the RWizard environment. KnobR uses the *specpool*, *estimate* and *specaccum* functions of the *vegan* package (Oksanen *et al.*, 2014) and the *ICE* function of the *fossil* package (Vavrek, 2014).

A spatial unit size of 15 x 15 minutes was chosen as a good compromise to display the map results, resulting in a total of 98 spatial units. Further arguments were as follows: method= "incidence" (presence-absence data), cutoff (threshold representing the ratio between the number of database records and the number of species. If this ratio was lower than the selected threshold, the spatial unit was considered non-informative) = 1; cutoff Completeness (if the value of completeness was lower than this threshold, the spatial unit was also considered non-informative) = 10.

**Table 1.** Asymptotic species richness estimators for the global occurrences dataset of soft-bottom demersal fish in the Colombian Caribbean shelf and slope (García and Armenteras 2015, GBIF). Estimations were obtained using the free online software SpadeR (Chao *et al.* 2015).

Index	Estimate	95 % lower limit	95 % upper limit
Chao1	664	646	670
Chao1-bc	663	645	697
iChao1	672	660	690
ACE	655	643	676
ACE-1	659	645	683
First-order Jackknife	683	666	709
Second-order Jackknife	698	670	745

Performance of the available estimators of asymptotic richness in KnobR for incidence data (Chao, ICE, first order jackknife, second order jackknife and bootstrap) was examined. The ICE estimator was excluded from further consideration as the estimates obtained were unrealistic. For instance, for a spatial unit with 44 observed species this estimator predicted an asymptotic richness as high as 2450 species. The other estimators provided plausible values ranging from an average of 99 (bootstrap) to 265 (Chao) predicted species per spatial unit for an average of 79 observed species per spatial unit. The performance of asymptotic species richness estimators depends on a variety of assemblage attributes (e.g., species abundance distribution, spatial aggregation and species detection probability), sampling design and effort (Reese *et al.*, 2014). Sources of the georeferenced occurrences are heterogeneous, although each were based on bottom trawling, in the sense that they included a diverse array of surveys and cruises with different field designs and spatial and temporal coverage (García and Armenteras, 2015). Thus, since the suitability of any one estimator over the other cannot be evaluated, the estimation of asymptotic richness used per spatial unit was chosen to be the mean value of the estimators excluding ICE.

Furthermore, the global estimation of richness and completeness for the entire dataset (the entire shelf and slope) was assessed using the free online software SpadeR (Chao *et al.*, 2015). For this, data were treated as of the “species frequency” type, equating the number of occurrences per species with their frequency.

In order to highlight locations with the highest observed and predicted richness along the Colombian Caribbean

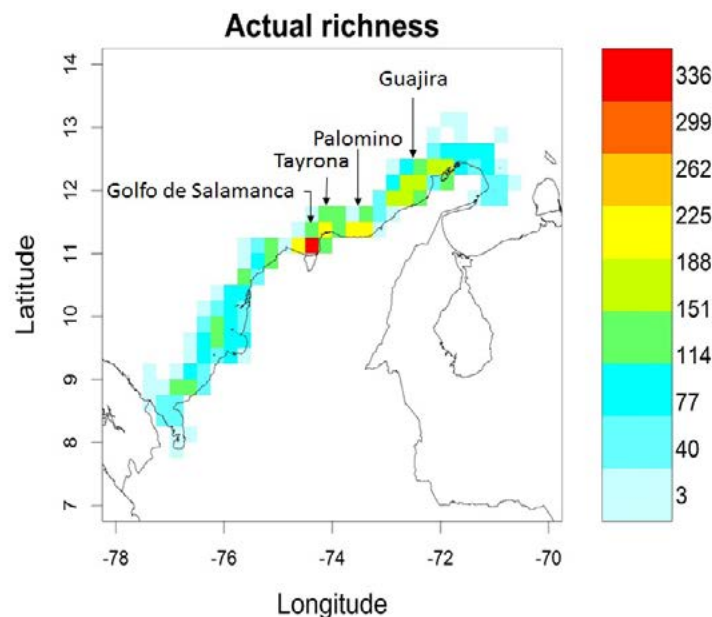
coast, the zonification (ecoregions, in their terminology) scheme in Acero and Díaz (2003) were used.

Two cartilaginous fish species included in the maps described by García and Armenteras (2015) were not included in the analysis: *Atlantoraja cyclophora* as its general distributions did not to include the Western Central Atlantic and *Pristis pectinata* due to its probably extinction in the Colombian Caribbean (Gómez-Rodríguez *et al.*, 2014).

## RESULTS

A total of 625 soft-bottom fish species, distributed over 15651 occurrences formed the basis of the analysis (81 % of which from sources in García and Armenteras (2015) and 19 % from GBIF). The species list is given in Online Resource 1. Table 1 shows the asymptotic richness predicted by different indices for the complete dataset. Indices ranged from 655 species estimated by ACE to 698 species estimated by the second order jackknife (Table 1). The estimates from each of the indices suggest that the global asymptotic species richness has not been reached, despite the spatial and temporal coverage and sampling intensity of the data (García and Armenteras, 2015). The mean indices estimate (Table 1) gave a value of 671 species, thus, around 46 species (93 % completeness) would remain to be registered in the soft-bottom habitat of the Colombian Caribbean shelf and slope.

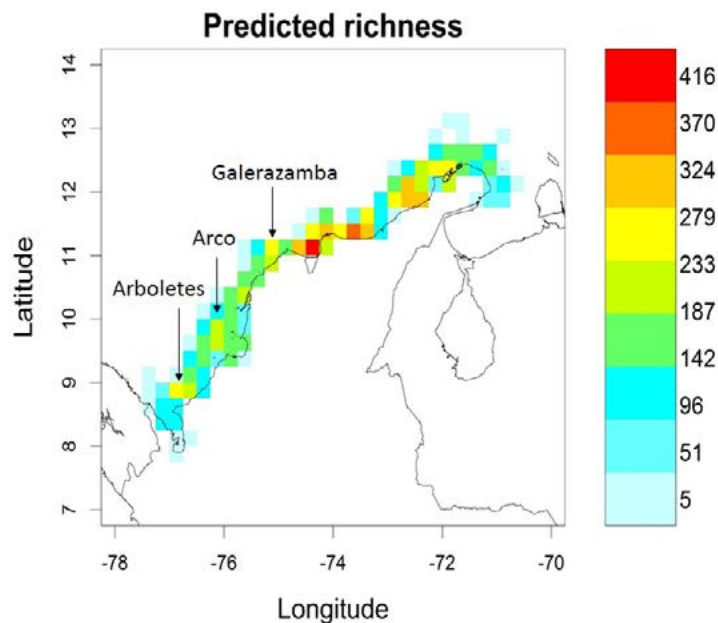
Figures 1, 2 and 3 show the observed distribution, predicted distribution and the spatial completeness of species richness, respectively, of soft-bottom fishes in the Colombian Caribbean Sea. In general, the northern shelf and slope shows higher observed and consequently predicted richness than the south (Figs. 1 and 2). The Golfo



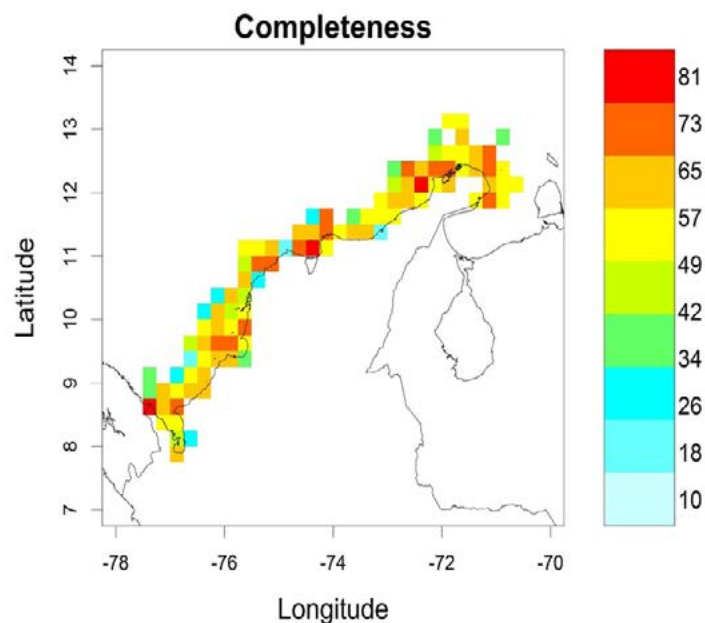
**Figure 1.** Observed distribution of soft-bottom fish species richness in the Colombian Caribbean shelf and slope. Spatial units are 15 x 15 minutes in size. The color scale refers to the species number range. Highlighted zones are those with high observed species richness.

de Salamanca zone stands out as the region with the highest species richness (Figs. 1 and 2). Zones in the south such as Galerazamba, Arco (coralline archipelago) and Arboletes are predicted to have a greater number of species than those observed so far (Fig. 2).

The completeness values showed no apparent spatial pattern. No individual spatial unit reached 100 % completeness, including those in the Golfo de Salamanca zone (Fig. 3). Of the 98 spatial units just seven (7.4 %) reached 70 % completeness or higher. The mean spatial



**Figure 2.** Predicted soft-bottom fish species richness in the Colombian Caribbean Sea shelf and slope. The estimator of asymptotic species richness is the mean value obtained from the Chao, first-order jackknife, second-order jackknife and bootstrap indices per spatial unit, as calculated using the KnobR application. The color scale refers to the species number range. The highlighted zones are those with a relatively low to medium observed number of species but with a relatively high predicted species richness. Arco Zone= coralline archipelago. Spatial unit size is the same as in Fig. 1.



**Figure 3.** Spatial estimation of completeness (observed versus predicted species richness presented as a percentage) of the soft-bottom fish species richness inventory in the Colombian Caribbean shelf and slope. No spatial unit reached 100 % completeness. The color scale represents the percentage completeness range. Spatial unit size same as in Fig. 1.

unit completeness was found to be 54 % (13 % standard deviation).

In order to check for unevenness of research effort, multiple Spearman correlations were performed for the latitude, occurrences (number of records), observed richness, predicted richness and completeness of the spatial units. There were low correlations between latitude with the other variables, none of which were statistically significant ( $p > 0.05$ ,  $n = 98$ ) suggesting no spatial bias in research effort. As expected, the number of occurrences showed significant positive correlations with the observed and predicted species richness ( $p < 0.05$ ,  $n = 98$ ), which were unsurprisingly, significantly correlated ( $p < 0.05$ ,  $n = 98$ ).

Completeness was significantly correlated with occurrences and both the observed and predicted richness ( $p < 0.05$ ,  $n = 98$ ), although the correlation with predicted richness was low and negative (-0.223, Spearman index). Therefore, higher predicted richness was associated with lower completeness, suggesting that, in spatial terms, the richness of soft-bottom fish has not been fully surveyed.

## DISCUSSION

The number of fish species (625) recorded in García and Armenteras (2015) for soft bottoms only in the Colombian Caribbean is quite impressive. In contrast, the Mediterranean Sea harbors 650 species in all habitats (Coll *et al.*, 2010) while 230 species have been recorded in the North Sea in all habitats (Bloomfield *et al.*, 2009), both of which have much larger continental shelves than the Colombian Caribbean continental shelf.

The global list of species is coming to completeness but with room for new encounters (mean value of 93 % completeness). García and Armenteras (2015) analyzed completeness in terms of depth strata, finding that completeness was decreased in strata at greater depths. Thus, in the Colombian Caribbean, new species are more likely to be recorded in deep-sea habitats, although even for the shallowest strata (0-50 m) 100 % completeness was not obtained (García and Armenteras, 2015). The species richness distribution maps for soft-bottom demersal fish I presented in the current study is consistent with the map presented in Miloslavich *et al.* (2010), which represents species of a wide variety of taxa including fish, recorded in the Caribbean in spatial cells including the Colombian shelf. The areas of high species richness are similar in both the current study and that of Miloslavich *et al.* (2010), such as reported for Guajira, Golfo de Salamanca, among others (Figs. 1 and 2).

At the spatial scale used here (15 x 15 minutes spatial units) species inventory is partial (54 % completeness per spatial unit). The observation of a significant negative correlation between the predicted richness and completeness reinforces the suggestion of incompletely surveyed spatial

units. In the case of well-surveyed units, the expectation is that there would be no correlation between such variables. This was unexpected considering the comprehensive temporal (several decades) and spatial (entire continental shelf and slope with depths from 0 to 1800 m) coverage by García and Armenteras (2015). One possible explanation relates to the distribution of occurrences observed between species. Just 47 of the 625 fish species accumulated 40% of occurrences, and as many as 296 species showed ten or fewer occurrences in the dataset, representing slightly above 8 % of all occurrences. Most of these rare species also showed disjointed distribution (García and Armenteras, 2015). Consequently, for a given spatial unit, many of the species are rare resulting in predictions of high species richness but low completeness.

The biological reasons for commonest and rarity of species represents one of the paramount and still not fully resolved questions in ecology (Magurran, 2013). Hypothesis attempting to explain this pattern have oscillated between the neutral theory of Hubbell (2001) to attempts for unifying theories (McGill, 2010). However, the more parsimonious explanation suggested by Magurran and Henderson (2003) appears to be the most applicable for the current study. The current dataset includes temporal measurements, as the occurrences spans approximately five decades (García and Armenteras, 2015). Over such a long period, it is unlikely that the spatial distribution of rare fish species had remained static. Thus, it is plausible that the species found in any spatial unit can be divided into core and occasional species, according to the terminology in Magurran and Henderson (2003), whereby the dynamics of presence or absence over time for these occasional species may explain the poor level of completeness obtained for the spatial scale studied. In view of the temporal dimension embedded in the dataset the spatial distribution of species richness found here should be regarded as an average.

In the case of species richness being criteria for the formulation of MPAs, the results presented here may be informative for such initiatives in the Colombian Caribbean. Soft-bottom habitats, being an uncharismatic habitat, are poorly represented in MPAs in the Colombian Caribbean Sea (Segura-Quintero *et al.*, 2012). Although the Tayrona, Golfo de Salamanca and Arco zones found to be among those with a high observed and/or predicted species richness (Figs. 1 and 2) partly overlap with protected areas, there are currently no dedicated soft-bottom MPAs in the Colombian Caribbean Sea, with the exception of Corales de Profundidad (Arco zone). This zone is currently declared protected due to its rich diversity of deep sea corals on a mixed bottom, not because its fish richness (Alonso *et al.*, 2015). To my knowledge, the only proposal for soft-bottom MPAs in the Colombian Caribbean is that by Páramo *et al.*, (2009) who identified an area at the northern end of the Guajira zone as

having high species diversity (Shannon-Wiener index) where I predict relatively high species richness, and an area in the Palomino zone on the ground that juvenile fish prevail there, and where I observe and predict high species richness (Figs. 1 and 2).

I studied a subset of the dataset corresponding to elasmobranchs (sharks and rays) using the same approach as here (García, 2017). Interestingly, the spatial pattern of elasmobranchs species richness roughly coincides with the findings for the complete dataset, although elasmobranchs amount to about 10% of the species (63 species, García, 2017) in the dataset. Thus, managing and protecting bony and cartilaginous fishes may be achieved under the same schema.

Future research should seek to increase the number of MPAs in the Colombian Caribbean. These should: (1) increase inclusion of soft-bottom habitats more extensively as they represent a rich species habitat, in addition to being of central importance for the food security of local communities (García, 2010); and (2) focus on areas identified here and by García (2017) as having a high observed and/or predicted fish species richness. However, the formal declaration of a MPA is no guarantee of real protection as MPAs in Colombia face governance problems (Ramírez, 2016). Nevertheless, the results presented here are necessary for such an endeavour.

## CONCLUSIONS

The study reveals a rich fish fauna in soft-bottoms habitats in the Colombian Caribbean. Globally the species list is coming to completion but at smaller spatial scales species rich knowledge is far from complete even in shallow depths. Several zones were identified as having high richness while others were predicted to have high richness. In view of the results, marine protected areas should extend to soft-bottom habitats, so far neglected in this context.

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## CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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