

Factors affecting species richness of marine elasmobranchs

Cástor Guisande · Bernardo Patti · Antonio Vaamonde ·
Ana Manjarrés-Hernández · Patricia Pelayo-Villamil ·
Emilio García-Roselló · Jacinto González-Dacosta ·
Jürgen Heine · Carlos Granado-Lorencio

Received: 14 February 2013 / Accepted: 6 June 2013 / Published online: 15 June 2013
© Springer Science+Business Media Dordrecht 2013

Abstract Many studies on elasmobranchs, sharks and batoids (rays, skates and guitarfishes), have focused on the factors responsible for biomass decline, but little attention has been paid to the factors that affect species richness. We used the software package ModestR to determine the geographical distribution of all valid marine elasmobranch species (512 species of sharks and 619 species of batoids), thereby making it possible to determine the species composition of the elasmobranch community in any area worldwide. The

Electronic supplementary material The online version of this article (doi:[10.1007/s10531-013-0507-3](https://doi.org/10.1007/s10531-013-0507-3)) contains supplementary material, which is available to authorized users.

C. Guisande (✉)

Facultad de Ciencias, Universidad de Vigo, Lagoas-Marcosende, 36200 Vigo, Spain
e-mail: castor@uvigo.es

B. Patti

Istituto per l'Ambiente Marino Costiero, U.O. Capo Granitola, Consiglio Nazionale delle Ricerche,
Via del Mare 3, Campobello di Mazara, TP 91021, Italy

A. Vaamonde

Departamento de Estadística e Investigación Operativa Facultad de CCEE y Empresariales,
Universidad de Vigo, Torrecedeira 105, 36208 Vigo, Spain

A. Manjarrés-Hernández

Instituto Amazónico de Investigaciones-IMANI, Universidad Nacional de Colombia, A.A. 215 Leticia,
Colombia

P. Pelayo-Villamil

Grupo de Ictiología, Universidad de Antioquia, Medellín A.A. 1226, Colombia

E. García-Roselló · J. González-Dacosta · J. Heine

Departamento de Informática, Edificio Fundación, Universidad de Vigo, Campus Lagoas-Marcosende,
36310 Vigo, Spain

C. Granado-Lorencio

Departamento de Biología Vegetal y Ecología Facultad de Biología, Universidad de Sevilla, Sevilla,
Spain

primary aim of this study was to identify the factors associated with the species richness of elasmobranchs. The data were analyzed using multiple regressions and Support Vector Machine (SVM) in cells of $1^\circ \times 1^\circ$ with the analyzed abiotic variables being bathymetry, chlorophyll *a*, sea surface temperature, photosynthetically available radiation, pH, cloud cover, the concentrations of calcite, silicate, phosphate and nitrate, salinity, particulate organic carbon, diffuse attenuation and dissolved oxygen. The mean area of occupancy of the species was used as an indicator of niche occupancy. The model performed with SVM explained 97 and 99 % of the variance observed in the species richness of batoids and sharks, respectively. Mean area of occupancy, temperature and bathymetry were the variables with a higher contribution to the variance observed in both sharks and batoids. The negative residuals of the model performed with SVM indicated areas with lower than predicted species richness. These may be potential areas with undiscovered and/or unregistered species, or areas with decreased species richness due to the negative effect of anthropogenic factors, i.e. overfishing

Keywords Sharks · Batoids · Species richness · Area of occupancy

Introduction

Fishing pressure due to target or non-target (bycatch) fisheries has depleted elasmobranch populations worldwide (Baum et al. 2003; Barker and Schluessel 2005; Ward and Myers 2005; Clarke et al. 2006; Heithaus et al. 2008; Dulvy et al. 2008; Ferretti et al. 2008, 2010). In addition to the intrinsic economic importance of elasmobranchs, depletion of their populations could have cascading effects on the food web, particularly in coastal ecosystems (Stevens et al. 2000), with unforeseen consequences for the biomass, productivity, and community composition of lower trophic levels (Frank et al. 2006).

Ecologically sensitive bycatch species are of particular concern, because they may decline more rapidly than target species (Myers and Worm 2005). Moreover, the disappearance of large, conspicuous bycatch species can go unchecked and unnoticed (Casey and Myers 1998). Reasons for the pronounced sensitivity of sharks and batoids (rays, skates and guitarfishes) to fishing pressure are their large body size coupled with low fecundity, low reproductive rates and high age at maturity, which result in low recovery rates from exploitation for these sensitive species (Casey and Myers 1998; Dulvy and Reynolds 2002; Dulvy et al. 2003; Field et al. 2010).

Overfishing may also result in a reduction in species richness (Greenstreet and Rogers 2006). In order to better understand the potential anthropogenic effects on the diversity of elasmobranchs, it is first necessary to elucidate the general relationships between the diversity of fish communities and environmental factors. Knowledge of the species richness of a community in a geographical region should be the initial basis for any long term program of sustained conservation. The primary factors that govern the species richness of elasmobranchs, however, remain unknown.

A study on the factors that control species richness requires information about the distribution of species. The vast geographic scale of pelagic marine ecosystems together with the widespread distribution of some elasmobranch species, has constrained our ability to adequately determine the geographical distribution of elasmobranchs. Lucifora et al. (2011) synthesized fragmented information on the distributions of sharks to create the first

global shark diversity pattern. However, there is no such synthesis for batoid fishes. Therefore, the first aim of this study was to develop range maps of all valid species of elasmobranchs (1128 species) using ModestR (www.ipez.es/ModestR).

The second aim of this study was to determine the main factors related to the species richness of elasmobranchs. In addition to abiotic factors such as temperature, bathymetry, nutrient concentration, etc., we also included biotic factors in the models. One of the hypotheses proposed to explain species richness is the Rapoport rescue effect (Stevens 1989). Rapoport's rule predicts that species occupy broader ranges at higher latitudes, and as such, mean latitudinal range size enlarges with increasing latitude (Rapoport 1982). The relationship between the latitudinal pattern in species richness and average species range size may be the outcome of the same underlying mechanism; that the breadth of habitat becomes larger as the area of occupancy of the species increases (Pagel et al. 1991; Eeley and Foleys 1999). Rapoport's rule has been studied in marine teleosts, although some studies do not support the hypothesis (Rohde et al. 1993) but other studies do support it (Fortes and Absãlo 2010), and it has been not tested in elasmobranchs. For this reason, we included the area of occupancy of the species in the models as a potential indicator of niche occupancy and, hence, of competition among the species.

Finally, the third aim was to compare the research effort among areas, because there is the possibility of an increasing species diversity as a consequence of increasing research effort (Simboura and Zenetos 2005). Therefore, in addition to the effect of the abiotic and biotic factors, part of the variance in species richness of the elasmobranchs might be due to differences in research effort among areas resulting in different success in registering and/or finding new species.

Materials and methods

Species distributions

We used ModestR (available free at the website <http://www.ipez.es/ModestR>), to develop the range maps of the species according to the protocol explained by Pelayo-Villamil et al. (2012). To accomplish this, we created a dataset called Elasmobranchii.DB, also available at the noted web page, with the geographical distribution of all valid marine species of elasmobranchs currently recognised by systematists (Eschmeyer and Fricke 2013) and available in IPEZ (<http://www.ipez.es/index%20ingles.html>; Guisande et al. 2010): 512 species of sharks and 619 species of batoids (see Appendix). We did not include the freshwater species *Dasyatis laosensis*, *Makararaja chindwinensis* and the 25 species of the family Potamotrygonidae. We did not include species that are known but undescribed. For a given area, we did not include either those species regarded only as potentially present or those for which there were doubts about its presence. Once the information had been introduced into Elasmobranchii.DB, it was possible to obtain the species list and, therefore, also the number of species (species richness), of elasmobranchs in any area worldwide with ModestR.

Species distributions were obtained by consulting multiple different sources (Fischer et al. 1981, 1987, 1995; Whitehead et al. 1984; Compagno 1984; Lloris and Rucabado 1998; Bellemans et al. 1988; Schneider 1990; Cervigon et al. 1992; Bianchi et al. 1999; Carpenter and Niem 1999; Bonfil and Abdallah 2004; Serena 2005; Compagno et al. 2005; IUCN 2012; GBIF 2013; Froese and Pauly 2013; Eschmeyer and Fricke 2013; Guisande et al. 2012). For those species that have been described in recent years with no information

available from field guides or websites, we reviewed all publications with relevant information on the distribution of the species. These are not listed here due to the large number of citations, but are shown in the Appendix. Therefore, our range maps are expert maps and no maps based on species distribution models.

Environmental variables

The Bio-ORACLE global dataset 90°N–90°S real values were used as environmental factors (Tyberghein et al. 2012). This dataset includes the mean values from 2002 to 2009 in cells of $5' \times 5'$ of the following variables: calcite concentration (mol m^{-3}), chlorophyll *a* (mg m^{-3}), sea surface temperature ($^{\circ}\text{C}$), silicate ($\mu\text{mol l}^{-1}$), salinity (PSS), phosphate ($\mu\text{mol l}^{-1}$), pH, photosynthetically available radiation ($\text{Einstein m}^{-2} \text{day}^{-1}$), nitrate ($\mu\text{mol l}^{-1}$), cloud cover (%), diffuse attenuation (m^{-1}) and dissolved oxygen (ml l^{-1}).

In addition the variables mentioned above, Particulate Organic Carbon (POC) data were also used here in as estimated and provided from the NASA MODIS-Aqua Mission, distributed as a Level-3 Standard Mapped Image product, reprocessing No. 2012.0 (Feldman and McClain 2013). Specifically, the entire mission composite, covering the period 4 July 2002–31 December 2012, was downloaded from the <http://oceancolor.gsfc.nasa.gov/cgi/l3> website as Standard Mapped Image File in Hierarchical Data Format (HDF) at 5 min resolution (about $9 \times 9 \text{ km}^2$).

Bathymetry data are from Terrainbase dataset, a 5-min resolution global ocean depth and land surface elevation dataset compiled by the U.S. National Geophysical Data Center (NGDC) and distributed by the Research Data Archive (RDA), which is maintained by the Computational and Information Systems Laboratory (CISL) at the National Center for Atmospheric Research (NCAR). NCAR is sponsored by the National Science Foundation (NSF). The original data are available from the RDA (<http://dss.ucar.edu>) in dataset number ds759.2.

Area of occupancy

ModestR also allows the export of statistics for each species as the area of occupancy (Gaston 1991). This was estimated from a rasterized map of $1' \times 1'$ cells (approximately $1.889 \times 1.852 \text{ km}$ at the equator), where the area of this cell in km^2 was estimated using the following equation:

$$1.852 * \frac{12756.2 * \pi}{21600} \cos\left(\text{latitude} * \frac{\pi}{180}\right)$$

Area index is the mean area of occupancies of all species that it can be estimated in cells from $60' \times 60'$ to $1' \times 1'$ with ModestR.

Statistical analyses

The data were analyzed using multiple regressions and Support Vector Machine (SVM) for regression. In all models the species richness, the environmental variables and the area of occupancy were log transformed. For model estimation purposes the available data resolution was downscaled to $1^{\circ} \times 1^{\circ}$, we worked with all world, therefore also with those areas in which species richness was zero, and the area of occupancy was not weighted.

Stepwise multiple regressions were performed with stats R package (R Development Core Team 2013). The relative contribution of each variable in the regressions was

estimated with the methods LMG (the r^2 contribution averaged over orderings among regressors) and Last (each variables contribution, also sometimes called usefulness) with the R package relaimpo (Groemping 2013). Kolmogorov–Smirnov test with Lilliefors correction was used to test for normality of residuals. Residuals from a linear regression or multiple regression must be independent, and Durbin–Watson statistic is used to detect the presence of autocorrelation violating this assumption. Breusch–Pagan test was used to test for homoscedasticity of residuals. The presence of multicollinearity, linear relationship among regressors, may be a main problem, causing instability of estimations. The variance inflation factor (VIF) quantifies the severity of multicollinearity, providing an index that measures how much the variance of an estimated regression coefficient is increased because of collinearity. Other assumptions about regression models (normality, independence and homoscedasticity of residuals, and absence of multicollinearity), all of them tested in this paper, affect to significance tests, but goodness of fit can be simply evaluated through high proportion of explained variance (near 100 % in this work). No more assumptions are needed about species richness distribution.

SVM are supervised learning models with associated learning algorithms that analyze data and recognize patterns, and are used for classification and regression analysis. SVM enjoys excellent theoretical properties and a good performance under very general conditions. No strict assumptions are needed. We used the function `ksvm` of the package `kernlab` (Karatzoglou et al. 2013), which supports the well known C-svc, nu-svc, (classification) one-class-svc (novelty) eps-svr, nu-svr (regression) formulations along with native multi-class classification formulations and the bound constraint SVM formulations.

Results

Oceanic areas were at the lower end of species richness for elasmobranchs, whereas the highest values were observed in coastal regions (Fig. 1). Hotspots of diversity for sharks were in offshore areas in the south of Japan, Taiwan and China, eastern and western Australia, eastern South Africa, Mauritania and the Canary Islands. The species richness of batoids was greater from Morocco to the Congo, eastern South Africa, from India to southern China, Taiwan and southern Japan (Fig. 1).

Despite the fact that the number of species of batoids (619) was higher than the number of species of sharks (512), the number of shark species in the shark hotspots was almost double the number of species in the batoid hotspots (Fig. 1). Individual hotspots of species richness for sharks were located off southern Japan and Taiwan (more than 100 species per $5' \times 5'$ cell), whereas the maximum number of batoids in a hotspot was 58 species (from Morocco, Congo, eastern South Africa, India, southern China, Taiwan and southern Japan).

Since Linnaeus in 1758 described the first species of shark (*Prionace glauca*) and the first species of batoid fish (*Pristis pristis*), the cumulative species description curves for sharks and batoid fishes have not yet closely approached its asymptote (Fig. 2). There were three periods when the number of species described per year was higher than average (Fig. 2). Between 1838 and 1841 many elasmobranch species were described, although it was not due to intensive studies in any specific area, but mainly a consequences of the work of Müller and Henle (1838–1941) who described 33 species of batoid fishes and 28 shark species (11 species of the genus *Carcharhinus* among them). The geographical distribution of the species described between 1906 and 1913 showed that during that period intensive studies were conducted on sharks in Japan and south China. Finally, between

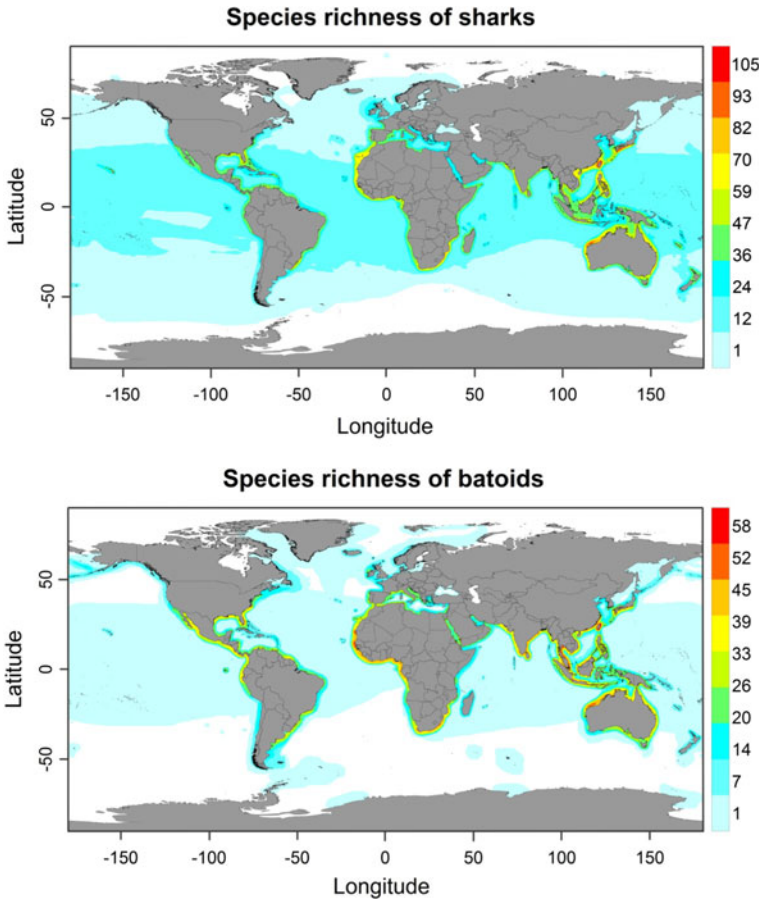
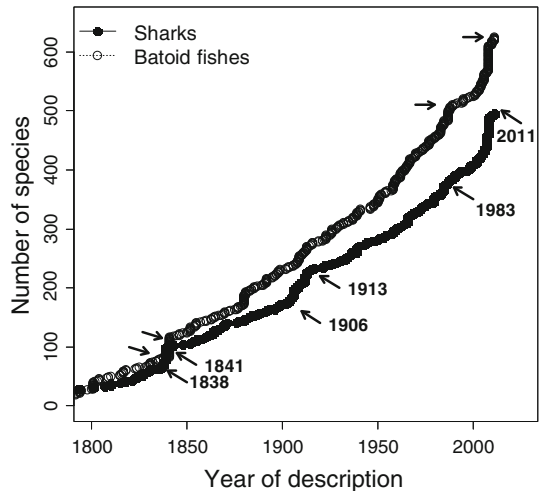


Fig. 1 Species richness of sharks and batoids around the world with a raster of $5' \times 5'$

1985 and 2012 many elasmobranchs species were described primarily due to the studies carried out in Australia and surrounding areas such as New Caledonia. Therefore, it seems that there were more taxonomic studies involving elasmobranchs in Australia and surrounding areas, south China and Japan than in other areas.

Dissolved oxygen was not included in any of the models because there was collinearity between this variable and sea surface temperature. Photosynthetically available radiation, chlorophyll *a*, pH, cloud cover, the concentration of calcite and diffuse attenuation were not significantly related with species richness in either model for batoids and sharks. The other variables (area of occupancy, bathymetry, sea surface temperature, silicate, salinity, phosphate, nitrate and POC) were significantly related with species richness and explained 74 and 89 %, of the variance observed in batoids and sharks, respectively, and 63 and 88 %, respectively without including the mean area of occupancy of the species. Figure 3 shows that the environmental variables with a higher contribution were area of occupancy, temperature and bathymetry for both batoids and sharks. Temperature, however, was more important for sharks and area of occupancy for batoids.

Fig. 2 Plot of cumulative species number as a function of the year of description for sharks and batoids. The arrows indicate the periods where the number of species described per year was higher than average



In both batoids and sharks the standardised residuals did not have a normal distribution (Shapiro–Wilk, $p < 0.001$), there was autocorrelation (Durbin–Watson, $p < 0.001$) but not homoscedasticity in the residuals (Breusch–Pagan test, $p < 0.001$). Therefore, it was not possible to test the significance of the regressions either for sharks nor batoids.

The coefficients of determination of the models performed with SVM showed that the variables used in the models explained the 97 and 99 % of the variance observed in the species richness of batoids and sharks, respectively, and 86 and 96 %, respectively without including the mean area of occupancy of the species.

The relationship between mean area of occupancy and species richness showed the same pattern for both sharks and batoids (Fig. 4). There were high values of the mean area of occupancy only in areas where species richness is low.

The residuals of the model performed with SVM regression showed areas with lower than predicted species richness observed than predicted. These may be possibly areas with undiscovered and/or unregistered species, or areas with lower species richness due to the negative effect of anthropogenic factors (Fig. 5). In sharks, these areas were located in Chile, Uruguay, Argentina, South Africa, Namibia, Gabon, western Sahara, the Arabian peninsula and also in Australia, China, Japan and surroundings areas despite, as mentioned above, the more intense research effort in the latter regions. The uniform green colour in the map indicates that most of averaged residuals were close to zero (Fig 5, upper panel).

The uniform yellow colour in the map of the averaged residuals of the SVM regression of batoids (Fig. 5, lower panel) also indicates that most residuals were close to zero. In the case of batoids, there were a few areas with negative values; these again being in Australia, southern Brazil and Uruguay, many central areas of the Mediterranean Sea, Namibia, Angola and northern Japan.

Discussion

Tittensor et al. (2010) examined global patterns and predictors of species richness across 13 major species groups, ranging from zooplankton to marine mammals, and concluded that sea surface temperature was the only environmental predictor strongly related to

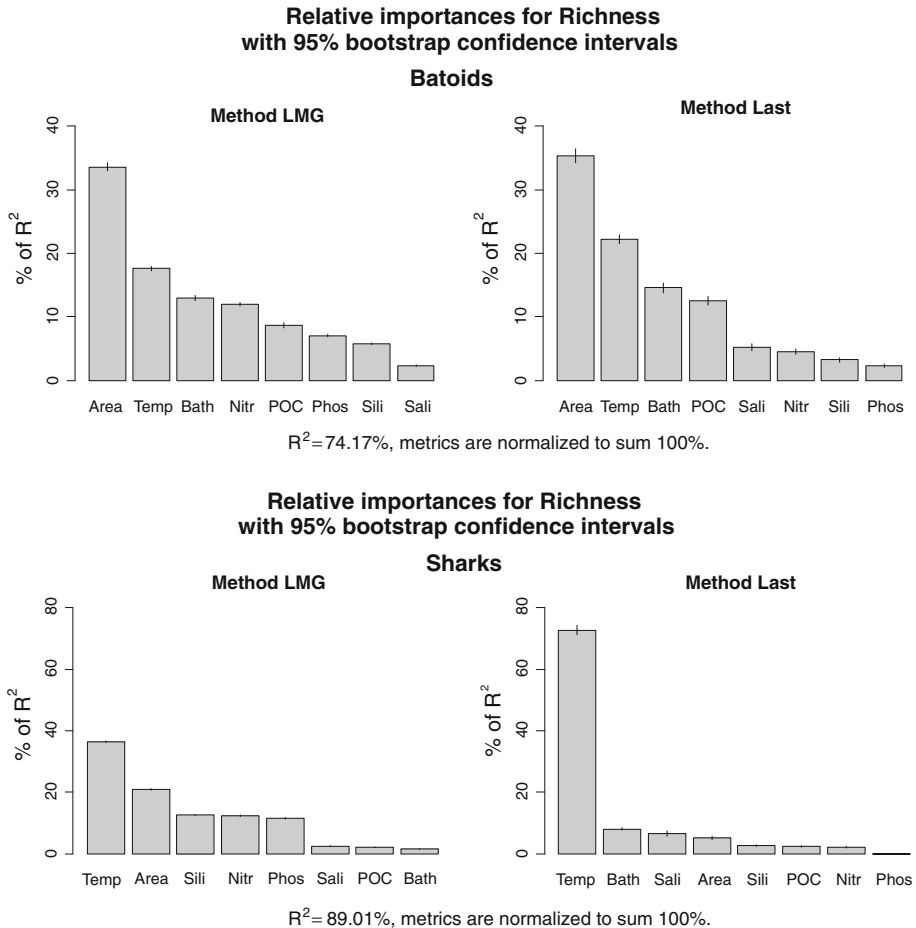


Fig. 3 Relative contribution of the variables in the multiple regressions obtained with LMG and Last methods. The dependent variable was species richness and the independent variables were area of occupancy, bathymetry, temperature, silicate, salinity, phosphate, nitrate and POC

diversity across all taxa. We also observed that temperature was an important predictor of species richness in elasmobranchs, particularly in sharks. The contribution of bathymetry to model prediction was also important in the case of batoids, probably because many batoids are slope associated species, and, thus mostly present in coastal areas.

One important contribution of our study was to demonstrate the importance of biotic factors. Most of the studies about species distribution models and the identification of the factors governing species richness have been focused on abiotic drivers, but it is also recognised that observed patterns of species occurrences are strongly influenced by biotic factors which should also be taken in consideration in species distribution studies (Guisan and Thuiller 2005). The inclusion of additional predictors that account for known competitors or facilitators may increase both our understanding of species range limits and the predictive power of models (see Pellissier et al. 2010). We demonstrated that the mean area of occupancy of the species, which was considered a indicator of competition among the

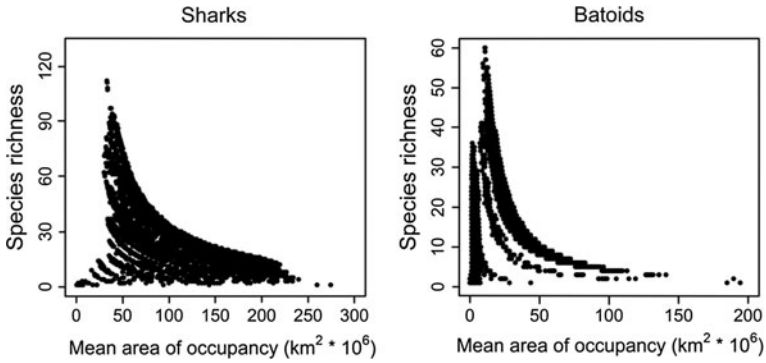


Fig. 4 Relationship between mean area of occupancy and species richness for both sharks and batoids in cells of $1^\circ \times 1^\circ$

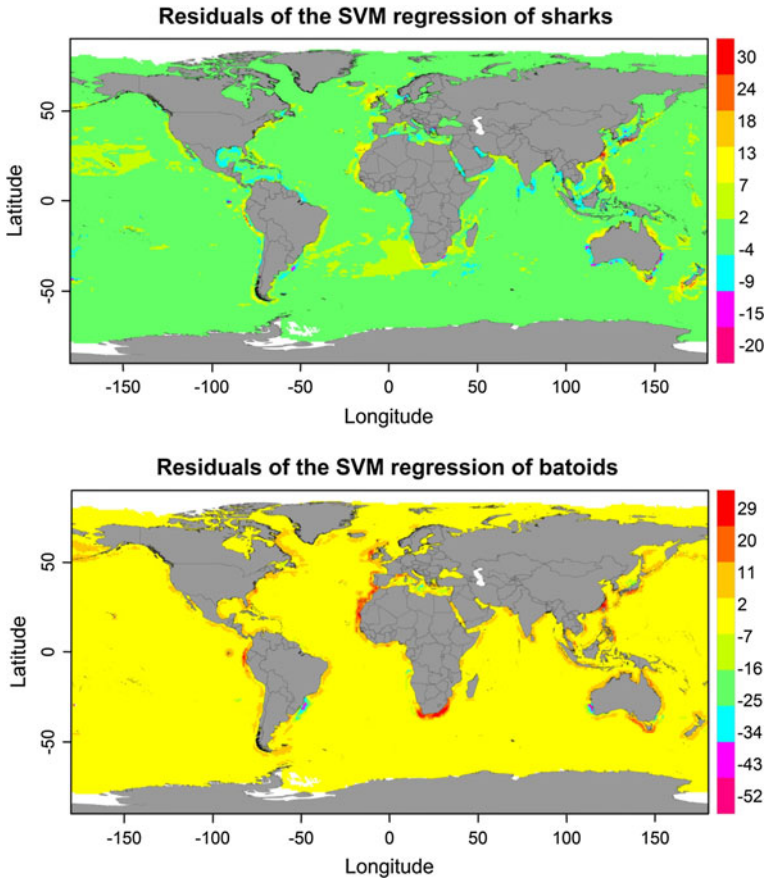


Fig. 5 Residuals of the SVM regressions of both sharks and batoids around the world in cells of $1^\circ \times 1^\circ$. Negative residuals indicate a lower number of observed species in the cell of $1^\circ \times 1^\circ$ than predicted by the model. The variables used in both models are mentioned in Fig. 3

species, was also a good proxy for predicting species richness, corroborating the hypothesis that higher number of species should lead to single species with a smaller geographic range size (Pagel et al. 1991; Eeley and Foleys 1999). The contribution of the area of occupancy to the model was more important in batoids than in sharks. This is probably due to the fact that most batoids are benthic animals and, hence, competition for space may limit their distributions.

The models explained the 97 and 99 % of the variance observed in species richness for batoids and sharks, respectively. Some part of the unexplained variance might be due to differences in research effort among areas resulting in different success in registering and/or finding new species or the negative effect of anthropogenic factors as overfishing. For this reason, we considered the negative residuals of the SVM regression as an potential indicator of areas with undiscovered and/or unregistered species, or areas with lower species richness due to the negative effect of anthropogenic factors. If this assumption is correct, Chile, Uruguay, Argentina, South Africa, Namibia, Gabon, western Sahara, the Arabian Peninsula, Mediterranean Sea, Namibia and Angola are potential areas with a lower number of species than expected according to habitat conditions. High negative values were also observed in areas where many taxonomic studies had been carried out, i.e. Australia and surroundings areas, which may be in this case an indication of unregistered rather than new species. It is also noteworthy that the expert maps overestimated the species richness in some oceanic areas (positive residuals), mainly close to central gyres, probably because those species considered to have a circumglobal distribution are in actuality not present in central oceanic areas. Although research effort and/or anthropogenic factors may partly be responsible of the unexplained variance, it is necessary to point out that other abiotic factors not included in the models and/or biotic factors such as source-sink dynamics, dispersal limitation or predation may also affect species richness. In any case, the unexplained variance was only 3 and 1 % in batoids and sharks, respectively.

In summary, our results show that the study of the range maps developed by experts and environmental variables available in the web allows the identification of the main factors governing species richness. Thanks to ModestR, that allows work with a large set of species, and facilities the elaboration of the expert maps, it is possible to export the species richness of any area around the world or just the cells of different size worldwide, and allows the estimation of area of occupancy. Our results corroborate previous findings that temperature is an important explanatory factor, but we also showed the important role of bathymetry and, particularly, the area of occupancy that seems to be a good indicator of competition among species.

References

- Barker MJ, Schluessel V (2005) Managing global shark fisheries: suggestions for prioritizing management strategies. *Aquatic Conserv* 15:325–347
- Baum JK, Myers RA, Kehler DG, Worm B, Harley SJ, Doherty PA (2003) Collapse and conservation of shark populations in the northwest Atlantic. *Science* 299:389–392
- Bellemans M, Sagna A, Fischer W, Scialabba N (1988) Fiches FAO d'identification des espèces pour les besoins de la pêche Guide des ressources halieutiques du Sénégal et de la Gambie (espèces marines et d'eaux saumâtres). FAO, Rome
- Bianchi G, Carpenter KE, Roux JP, Molloy FJ, Boyer D, Boyer HJ (1999) The living marine resources of Namibia FAO species identification field guide for fishery purposes. FAO, Rome
- Bonfil R, Abdallah M (2004) Field identification guide to the sharks and rays of the Red Sea and Gulf of Aden FAO. Species Identification Guide for Fishery Purposes. FAO, Rome

- Carpenter KE, Niem VH (1999) The living marine resources of the Western Central Pacific. FAO species identification guide for fishery purposes, vol 3. FAO, Rome
- Casey JM, Myers RA (1998) Near extinction of a large widely distributed fish. *Science* 281:690–692
- Cervigon F, Cipriani R, Fischer W, Garibaldi L, Hendrickx M (1992) Guía de campo de las especies comerciales marinas y de aguas salobres de la costa septentrional de Sur America. Fichas FAO de identificación de especies para los fines de la pesca. FAO, Rome
- Clarke SC, Murdoch K, Milner-Gulland EJ, Kirkwood GP, Michielsens CGJ, Agnew DJ, Pikitch EK, Nakano H, Shivji MS (2006) Global estimates of shark catches using trade records from commercial markets. *Ecol Lett* 9:1115–1126
- Compagno L (1984) Sharks of the world. An annotated and illustrated catalogue of shark species known to date. FAO, Rome
- Compagno L, Dando M, Fowler S (2005) Sharks of the world. Princeton University Press, Princeton
- Dulvy NK, Reynolds JD (2002) Predicting extinction vulnerability in skates. *Conserv Biol* 16:440–450
- Dulvy N, Sadovy Y, Reynolds JD (2003) Extinction vulnerability in marine populations. *Fish Fish* 4:25–64
- Dulvy N, Baum JK, Clarke S, Compagno LJ, Cortés E, Domingo A, Fordham S, Fowler S, Francis MP, Gibson C, Martínez J, Musick JA, Soldo A, Stevens JD, Valenti S (2008) You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquat Conserv* 18:459–482
- Eeley HAC, Foleys RA (1999) Species richness, species range size and ecological specialisation among African primates: geographical patterns and conservation implications. *Biodivers Conserv* 8:1033–1056
- Eschmeyer WN, Fricke R (eds) (2013) Catalog of fishes electronic version (June). <http://researchcalacademyorg/ichthyology/catalog/fishcatmain.asp>
- Feldman GC, McClain CR (2013) Ocean Color Web. In: Kuring N, Bailey S (eds) W MODIS-Aqua Reprocessing 2012.0, NASA Goddard Space Flight Center, Greenbelt. <http://oceancolor.gsfc.nasa.gov/>
- Ferretti F, Myers RA, Serena F, Lotze HK (2008) Loss of large predatory sharks from the Mediterranean Sea. *Conserv Biol* 22:952–964
- Ferretti F, Worm B, Britten GL, Heithaus MR, Lotze HK (2010) Patterns and ecosystem consequences of shark declines in the ocean. *Ecol Lett* 13:1055–1071
- Field IC, Meekan MG, Buckworth RC, Bradshaw CJA (2010) Susceptibility of sharks, rays and chimaeras to global extinction. *Adv Mar Biol* 56:275–363
- Fischer W, Bianchi G, Scott WB (1981) Eastern Central Atlantic (fishing areas 34, 47). FAO species identification sheets for fishery purposes. FAO, Rome
- Fischer W, Bauchot ML, Schneider M (1987) Fiches FAO d'Identification des Espèces pour les Besoins de la Peche Revision 1 Méditerranée et Mer Noire Zone de Pêche 37 Vol 2 Vértébrés. FAO, Rome
- Fischer W, Krupp F, Schneider W, Sommer C, Carpenter KE, Niem V (1995) Guía FAO para la identificación de especies para los fines de la pesca. Pacífico Centro-Oriental. FAO, Rome
- Fortes RR, Absão RS (2010) The latitudinal and bathymetric ranges of marine fishes: a global analysis to test the application of Rapoport's Rule. *Mar Ecol* 31:483–493
- Frank KT, Petrie B, Shackell NL, Choi JS (2006) Reconciling differences in trophic control in mid-latitude marine ecosystems. *Ecol Lett* 9:1096–1105
- Froese R, Pauly D (2013) FishBase. World Wide Web electronic publication, version (04/2013). <http://www.fishbase.org>
- Gaston KJ (1991) How large is a species' geographical range? *Oikos* 61:434–438
- GBIF (2013) GBIF data portal. <http://datagbif.org>
- Greenstreet SPR, Rogers SI (2006) Indicators of the health of the North Sea fish community: identifying reference levels for an ecosystem approach to management. *ICES J Mar Sci* 63:573–593
- Groemping U (2013) Relative importance of regressors in linear models. R package version 2.2. <http://CRAN.R-project.org/package=relaimpo>. Accessed 15 Feb 2013
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8:993–1009
- Guisande C, Manjarrés-Hernández A, Pelayo-Villamil P, Granado-Lorencio C, Riveiro I, Acuña A, Prieto-Piraquive E, Janeiro E, Matías JM, Patti C, Patti B, Mazzola S, Jiménez LF, Duque S, Salmerón F (2010) IPEz: an expert system for the taxonomic identification of fishes based on machine learning techniques. *Fish Res* 102:240–247
- Guisande C, Pascual PJ, Baro J, Granado-Lorencio C, Acuña A, Manjarrés-Hernández A, Pelayo-Villamil P (2012) Tiburones, rayas, quimeras, lampreas y mixínidos de la costa atlántica de la Península Ibérica y Canarias. Ed. Díaz de Santos, Madrid, p 262
- Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. *Trends Ecol Evol* 23:202–210

- IUCN (2012) The IUCN Red List of Threatened Species. Version 2012.2. <http://www.iucnredlist.org>. Accessed 17 Oct 2012
- Karatzoglou A, Smola A, Hornik K (2013) Kernel-based Machine Learning Lab. R package version 0.9-15. <http://CRAN.R-project.org/package=kernlab>. Accessed 19 April 2013
- Lloris D, Rucabado J (1998) Guide d'Identification des Ressources Marines Vivantes du Maroc. Guide FAO d'identification des espèces pour les besoins de la pêche. FAO, Rome
- Lucifora LO, García VB, Worm B (2011) Global diversity hotspots and conservation priorities for sharks. *PLoS One* 6:1–7
- Müller J, Henle FJG (1838–1941) Systematische Beschreibung der Plagiostomen. Veit und Comp., Berlin. Systematische Beschreibung der Plagiostomen i–xxii:1–200
- Myers RA, Worm B (2005) Extinction, survival or recovery of large predatory fishes. *Phil Trans R Soc B* 360:13–20
- Page M, May R, Collie A (1991) Ecological aspects of the geographical distribution and diversity of mammalian species. *Am Nat* 137:791–815
- Pelayo-Villamil P, Guisande C, González-Vilas L, Carvajal-Quintero JD, Jiménez-Segura LF, García-Roselló E, Heine J, González-Dacosta J, Manjarrés-Hernández A, Vaamonde A, Granado-Lorencio C (2012) ModestR: Una herramienta informática para el estudio de los ecosistemas acuáticos de Colombia. *Act Biol* 34:225–239
- Pellissier P, Bräthen KA, Pottier J, Randin CF, Vittoz P, Dubuis A, Yoccoz NG, Alm T, Zimmermann NE, Guisan A (2010) Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. *Ecography* 33:1004–1014
- R Development Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rapoport EH (1982) Areography: geographic strategies of species (translation by B. Drausel). Pergamon, Oxford
- Rohde K, Heap M, Heap D (1993) Rapoport's rule does not apply to marine teleosts and cannot explain latitudinal gradients in species richness. *Am Nat* 142:1–16
- Schneider W (1990) Field guide to the commercial marine resources of the Gulf of Guinea. FAO species identification sheets for fishery purposes. FAO, Rome
- Serena F (2005) Field identification guide to the sharks and rays of the Mediterranean and Black Sea. FAO species identification guide for fishery purposes. FAO, Rome
- Simboura N, Zenetos A (2005) Increasing polychaete diversity as a consequence of increasing research effort in Greek waters: new records and exotic species. *Mediterr Mar Sci* 6(1):75–88
- Stevens GC (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am Nat* 133:240–256
- Stevens JD, Bonfil R, Dulvy NK, Walker P (2000) The effects of fishing on sharks rays and chimaeras (chondrichthyans) and the implications for marine ecosystems. *ICES J Mar Sci* 57:476–494
- Tittensor DP, Mora C, Walter J, Lotze HK, Ricard D, Berghe EV, Worm B (2010) Global patterns and predictors of marine biodiversity across taxa. *Nature* 466:1098–1101
- Tyberghein L, Verbruggen H, Pauly K, Troupin C, Mineur F, de Clerck O (2012) Bio-ORACLE: a global environmental dataset for marine species distribution modelling. *Global Ecol Biogeogr* 21:272–281
- Ward P, Myers RA (2005) Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. *Ecology* 86:835–847
- Whitehead PJP, Bauchot ML, Hureau JC, Nielsen J, Tortonese E (1984) Fishes of the North-eastern Atlantic and The Mediterranean, vol I–III. UNESCO, Paris