Review

Ecological niche models and species distribution models in marine environments: A literature review and spatial analysis of evidence

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ABSTRACT

In recent years, the use of ecological niche models (ENMs) and species distribution models (SDMs) to explore the patterns and processes behind observed distribution of species has experienced an explosive growth. Although the use of these methods has been less common and more recent in marine ecosystems than in a terrestrial context, they have shown significant increases in use and applications. Herein, we provide a systematic review of 328 articles on marine ENMs and SDMs published between 1990 and 2016, aiming to identify their main applications and the diversity of methodological frameworks in which they are developed, including spatial scale, geographic realm, taxonomic groups assessed, algorithms implemented, and data sources. Of the 328 studies, 48 % were at local scales, with a hotspot of research effort in the North Atlantic Ocean. Most studies were based on correlative approaches and were used to answer ecological or biogeographic questions about mechanisms underlying geographic ranges (64 %). A few attempted to evaluate impacts of climate change (19 %) or to develop strategies for conservation (11 %). Several correlative techniques have been used, but most common was the machine-learning approach Maxent (46 %) and statistical approaches such as generalized additive models GAMs (22 %) and generalized linear models, GLMs (14 %). The groups most studied were fish (23 %), molluscs (16 %), and marine mammals (14 %), the first two with commercial importance and the last important for conservation. We noted a lack of clarity regarding the definitions of ENMs *versus* SDMs, and a rather consistent failure to differentiate between them. This review exposed a need to know, reduce, and report error and uncertainty associated with species' occurrence records and environmental data. In addition, particular to marine realms, a third dimension should be incorporated into the modelling process, referring to the vertical position of the species, which will improve the precision and utility of these models. So too is of paramount importance the consideration of temporal and spatial resolution of environmental layers to adequately represent the dynamic nature of marine ecosystems, especially in the case of highly mobile species.

1. Introduction

Ecological niche models (ENMs) and species distribution models (SDMs) are commonly used in theoretical and applied studies in ecology and biogeography (Peterson et al., 2015). Among the most common applications are determining suitable sites for species (Guisan and Zimmermann, 2000), predicting impacts of future climate change on species' distributions (Pearson and Dawson, 2003), evaluating the invasive potential of non-native species (Jiménez-Valverde et al., 2011), and conservation planning (Guisan et al., 2013).

Three main categories of models are recognized in this field: correlative models, the most common in the literature, which estimate the ecological requirements of species by relating their known geographic distributions to a set of environmental variables (Araújo and Guisan, 2006; Franklin, 2009); mechanistic models that use detailed physiological information and first principles of biophysics (Kearney and Porter, 2009); and process-oriented models, which estimate distributions of species in terms of processes, including dispersal capability and biotic interactions (Peterson et al., 2015).

Throughout the history of modelling species' niches and distributions, such models have received a variety of names: "bioclimatic envelope models" (Araújo and Peterson, 2012), "habitat suitability models" (Hirzel et al., 2006), "species distribution models" (Elith and Leathwick, 2009), and "ecological niche models" (Peterson, 2006). This

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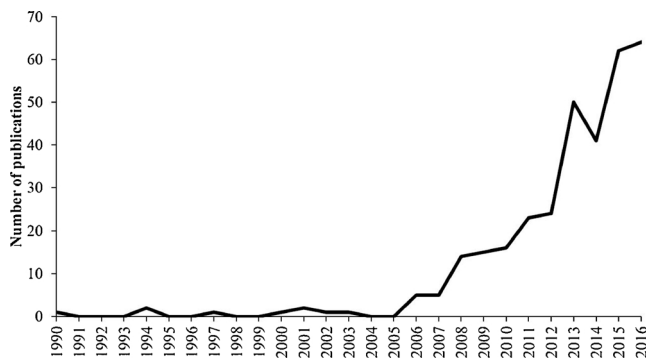 *E-mail address:* aliranoriega@gmail.com (A. Lira-Noriega).

Fig. 1. Trends in the number of publications per year about ENMs and SDMs applied to marine species.

panoply of terms has led to confusion and sometimes misinterpretation of model results (Peterson and Soberón, 2012; Soberón et al., 2017). More recently, two terms for two kinds of models has gained attention; acceptance is growing for the terms ENM and SDM as two distinct approaches to answering different questions (Peterson and Soberón, 2012). ENMs estimate fundamental niches of species, and are applied when the aim is to know the potential distribution, as in the case of invasive species or projections in space and time. On the other hand, SDMs attempt to estimate objects in geographic space, referring to actual distributions of species (Peterson and Soberón, 2012; Soberón et al., 2017).

Implementation of ENMs and SDMs started with terrestrial species, with increasing numbers of publications each year (Robinson et al., 2011). Their application to marine species has been less frequent, however, niche models applied to marine systems have become more popular in recent years (Fig. 1; Robinson et al., 2017).

Modelling marine species may be a challenge owing to the particular physical and biological characteristics of marine habitats and species (Robinson et al., 2011). One of the main challenges is the three-dimensionality of marine habitats, especially when modelling pelagic species living in the middle layers of the water column (Dambach and Rödder, 2011; Bentlage et al., 2013). This challenge is mainly imposed by the fact that most available environmental data layers describe the uppermost layers or the ocean floor (Assis et al., 2017a), and because of the limited knowledge of many pelagic organisms' ecology and behavior (Bentlage et al., 2013). Another important challenge is the dynamic nature of marine ecosystems, and the multiple spatial and temporal scales in which species-environment relationships occurs (Redfern et al., 2006; Scales et al., 2017). This dynamism is essential in the case of highly mobile species for which transitory environmental conditions may determine distribution over short time frames (Fernandez et al., 2017, 2018). Another particularity is the lack of hard physical barriers to dispersal. For most marine organisms, dispersal depends upon ocean currents, so, the inclusion of ocean currents in the models, or taking species dispersal into account, should enhance the development of more reliable models (Dambach and Rödder, 2011).

Previous efforts to summarize the state on the field of ENM and SDM in the marine realm include the works of Dambach and Rödder (2011) and Robinson et al. (2011) who provided overviews of marine niche modelling applications and highlighted the particular challenges in modelling marine environments such as three-dimensionality, species interactions and ontogenetic shifts. Vierod et al. (2014) reviewed applications of niche models in deep sea ecosystems that are considered vulnerable, pointing out data limitations and implications of model predictions, and paying special attention to sampling bias, spatial autocorrelation, spatial scale and model evaluation and validation; issues of paramount importance that are still under discussion in the field of modelling. Marshall et al. (2014) analyzed the use of these models in planning marine conservation; they highlighted the fact that in most

cases models related to marine ecosystems are not linked to management decisions, and about the need to use these models into spatial prioritization programs. Moreover, they recommend the use of models in combination with layers of human footprint to add value to the models for conservation purposes. Marcelino and Verbruggen (2015) reviewed the use of these techniques to model invasive seaweeds, and pointed out some particularities when modelling invasive species, such as the assumption that those species are in equilibrium with its environment and about the fact that they retain their ecological niche. Most recently, Robinson et al. (2017) reviewed applications of marine models and developed a framework to guide future applications through the use of a flow diagram to guide the process towards model implementation, calibration and validation.

This review aims to answer key questions related to use of ENMs and SDMs in marine ecosystems, on the basis of 328 research articles published on the topic between 1990 and 2016. For most cases, both ENMs and SDMs are herein referred to as "models", except when we want to emphasize differences between them. This is the most comprehensive review yet compiled for marine environments, as it includes information from previous reviews, plus new additions that have not been summarized previously. Here, we summarize applications of the models and the taxa that have been targets of modelling studies. We identify gaps in modelling of marine species and point out emerging trends in the field; we consider aspects of modelling that are specific to marine environments.

2. Ecological niche concepts in ENMs AND SDMs

Species distribution modelling and ecological niche modelling rely on ecological niche theory. The ecological niche of a species was originally defined as the suite of ecological conditions within which a species is capable of surviving and reproducing without immigrational subsidy (Grinnell, 1917). Later, the term was recycled to refer to the functional role that a species plays in a community (Elton, 1927). Still later, distinction was drawn between the fundamental niche, the set of abiotic environmental conditions under which a species is able to persist indefinitely, and the realized niche, the part of the fundamental niche that is constrained by interactions with other species (Hutchinson, 1957). As such, species' ranges can be conceived of as a consequence of three factors, (Soberón and Peterson, 2005): (i) presence of environmental (abiotic) conditions under which the species can establish, survive and reproduce; (ii) the biotic environment determined by the presence of species interactions such as competition or predation in which species can persist, and (iii) the area that is accessible to the species *via* its movement or dispersal capabilities. These restrictions have been captured in the so-called BAM diagram (Fig. 2. A): **B**, biotic; **A**, abiotic; **M**, movement (Soberón and Peterson, 2005), which has become a central concern in designing models (Barve et al., 2011; Saupe et al., 2012). Species geographic ranges are the result of the dynamic interactions of those three factors. In niche modelling, inclusion of **B** presents a problem owing to the complexity of biotic interactions, and estimation of **M** is a complex challenge, since it involves knowledge of areas that have been accessible to the species over relevant time periods (Barve et al., 2011). Hence, most correlative models have been restricted to representations of **A**.

Peterson et al. (2011) presented the Eltonian Noise Hypothesis, which is the idea that biotic interactions seldom constitute a significant constraint on the distributional potential of species on large geographic extents and low resolutions. This is also a hypothesis about biological processes and represents a simplification of modelling methodologies, considering the difficulties to include biotic interactions in the process. Biotic interactions are hard to measure and represent in a raster grid format (Soberón and Nakamura, 2009). For some species, ecological interactions may not play a dominant role at the coarse resolution typically used for modelling, and niche models have demonstrated a good performance in describing their distribution on the basis of **A** (Costa
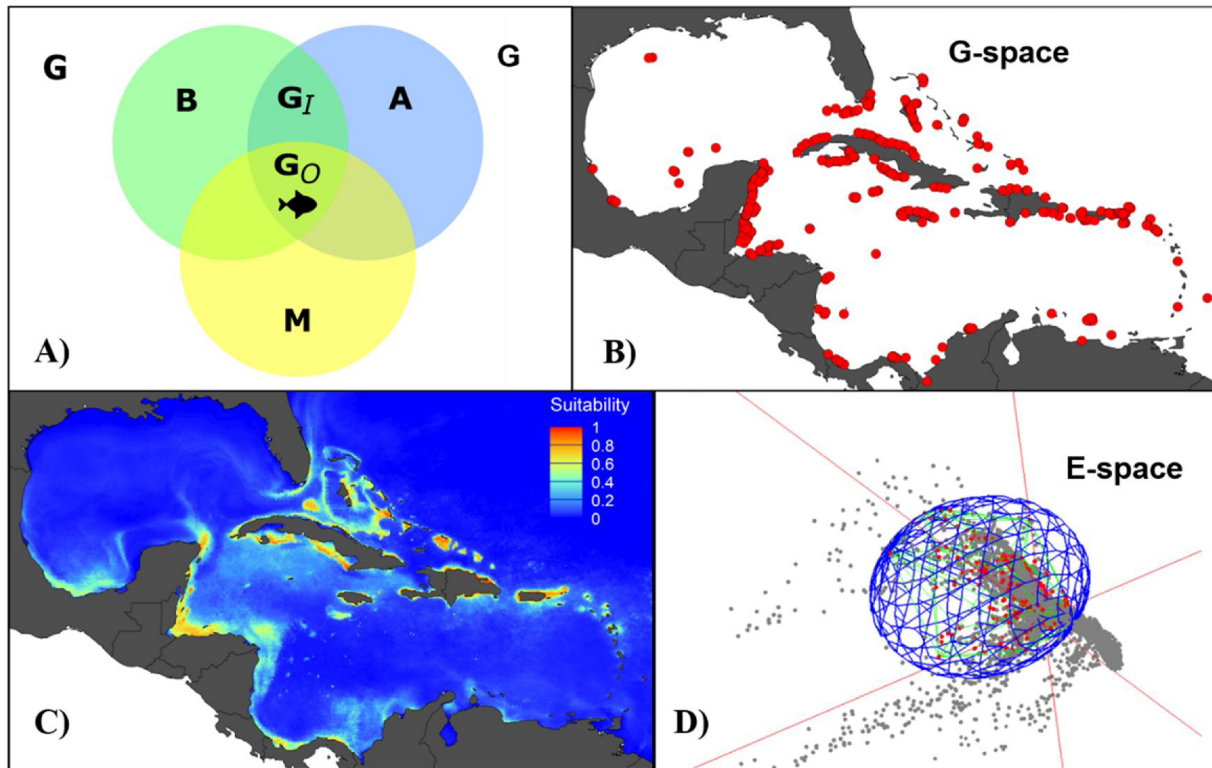
Fig. 2. A) BAM diagram representing the sets of factors influencing the geographic distribution of a species; **B**, represents the biotic conditions (*i.e.* coupled variables including biotic interactions appropriate for the species); **A**, region favorable for the species in terms of abiotic factors, typically used to represent limiting factors that would allow assessment of a species' fundamental niche (*e.g.* temperature and precipitation), and are typically of coarser spatial and temporal resolutions than biotic conditions; **M,** mobility or dispersal capacities of the species, encompassing the area that has been accessible for the species over relevant time periods (*e.g.* in a biogeographic context). G_O, occupied area, the actual area of distribution of the species where the three sets of components of the diagram intersect. G_I, invadable area, those places where biotic and abiotic conditions are adequate for species to survive but where the species has not yet reached because of some dispersal limitation. Modified from Soberón and Peterson (2005), and Soberón (2010). **B)** and **D)** are the representation of Hutchinson's duality: **B)** Occurrence localities for the scleractinian coral *Acropora palmata* obtained from OBIS and GBIF, representing the geographical space (G-space) occupied by the specie; **D)** three-dimensional model of the ecological niche of *A. palmata,* where gray dots represent all the environmental combinations (E-space) available in the Caribbean as a result of a principal component analysis, red dots represent the environments actually occupied by *A. palmata*, and the blue minimum-volume ellipsoid represents the fundamental ecological niche of *A. palmata*. **C)** Geographic projection of *A. palmata*'s niche model and corresponding suitability values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 2010; Lira-Noriega et al., 2013). Conversely, for some species it has been demonstrated that accounting for biotic interactions improves model capability at predicting their distributions (de Araújo et al., 2014)

Another important concept in niche theory applied to niche and distribution models is the so-called Hutchinson's duality, which refers to the correspondence between niche (*i.e.* environmental or ecological) and geographic (*i.e.* distributional) spaces (Fig. 2, B and D). According to this hypothesis, a region of the niche space may correspond to more than one place in the geographic space, whereas each point in the geographic space corresponds to exactly one point in niche space (Colwell and Rangel, 2009). This hypothesis is of great utility for explaining the differences between ENMs and SDMs concepts, which mistakenly are often termed as equivalent (Peterson and Soberón, 2012). For practical considerations SDM refers to the modelling objects in G-space, whereas ENM refers to modelling objects in E-space (Soberón et al., 2017). ENM requires an explicit estimation of the species' fundamental niche, and are intended to model the processes that shape the area of distribution of the species, and frequently used to transfer those causal factors into projections in space or time (Peterson and Soberón, 2012). SDM can only focus on the species' distribution, and ideally must restrict model calibration to accessible areas (M), account for true absences and incorporate dispersal and colonization capabilities (Peterson and Soberón, 2012). It is clear that there is an intimate relationship between these two concepts, and delimiting one

or the other may be confusing, but in order to let the field grow, it is important to be consistent and rigorous with the use of the terminology.

3. Literature search and analysis

3.1. Literature search

Using the ISI Web of Science and SCOPUS databases, we performed an exhaustive literature search using the keywords: "species distribution models*", "habitat suitability models*", "ecological niche models*", and "bioclimatic* envelope models*", each accompanied successively by the words "sea", "marine" and "ocean". The initial search, restricted to articles published during 1990–2016, yielded more than 2000 articles. We discarded articles that did not make explicit reference to modelling species distributions or ecological niches in a Grinnellian sense (Soberón, 2007), and those focused on biotic interactions (*e.g.* studies of trophic niches). Articles regarding mangrove ecosystems were also discarded, though we included studies of marine species able to live in estuaries and rivers. Additionally, we searched the "references" sections of each article for relevant publications that might not have been detected in the initial search. In total, 328 articles were selected to be included in this review (Appendix A).

3.2. Summary of information

Each article was entered in a database with author(s), publication year, study region, and the following fields:

3.2.1. Extent of analysis

In order to know the analytical extent of the studies, these were classified as locals if they cover the territory of one country or less (*e.g.* Portuguese coast), as regionals for two or more countries (*e.g.* Mediterranean Sea) and global if they were accomplished worldwide.

3.2.2. Taxonomic group

The classification of target species by taxonomic group did not focus on a particular taxonomic category to illustrate the great variety of organisms studied. Thus, categories include phylum, subphylum, and class, and less formal groups such as "seaweed". For the purpose of this review, elasmobranch is taken as a group separated from the category fish which includes the Actinopterygii class.

3.2.3. Source of occurrence data and environmental variables

We registered sources of occurrences data and environmental variables in modelling studies. We also recorded the environmental variables used in each study (*e.g.* wind velocity, water temperature).

3.2.4. Type of model and modelling technique

We classified the studies as correlative, mechanistic, or process-oriented. Since most studies were correlative, we further classified all articles depending on the modelling technique that they used (*e.g.* Maxent, GLM, ENFA).

3.2.5. Model selection and validation

In order to know how model selection and validation is done, we registered the procedures (*e.g.* cross-validation) and metrics (*e.g.* AUC, TSS) used in each article.

3.2.6. Aim of the studies

Studies were classified according to 9 topic categories: present potential distribution, climate change impacts, invasive species, distributions under past climates, abundance models (populations and communities), habitat use, evaluation of methods, conservation planning and management, and "other". The latter category includes testing niche conservatism, evolution, or niche reconstruction, and review articles. Articles addressing more than one research question were assigned to several categories if necessary.

Finally, in order to enlighten the geographic distribution of ENM and SDM efforts, the study area described in each article was digitized with GIS software using as a reference a 1° spatial resolution global grid. We extended this spatial representation to the modelling purposes and the taxonomic groups studied in the articles.

4. ENMs and SDMs in the marine realm

To our knowledge, this review of 328 articles is the most extensive overview of applications of SDM and ENM in the marine realm. We found a great variety of applications, species being modelled, environments being studied, and a broad geographic distribution of studies. Below, we attempt to describe the main findings of the literature reviewed.

4.1. Regions studied and extent of analysis

Each ocean was covered by at least 39 modelling exercises. Research in marine systems most frequently concerned the North Atlantic Ocean; hotspots of studies were along the northeastern coast of the United States, the west coast of Europe, and the Mediterranean Sea (Fig. 3). The least studied areas were the northwestern Pacific Ocean and the

Indian Ocean. Models have been used in all marine ecoregions (see also Robinson et al., 2017), with clear interest in the North Atlantic Ocean. Local studies predominated, followed by regional studies, only a few studies were at global scales (Fig. 4).

4.2. Taxonomic groups in marine modelling

Diverse marine taxonomic groups have been studied using ENMs or SDMs. Studies of fish and molluscs were most common (77 and 52 articles, respectively; Fig. 4). This concentration could be explained by the commercial importance that fisheries of those groups represent worldwide; according to the Food and Agriculture Organization of the United Nations (FAO), in 2015, fish and molluscs occupied first and second places, respectively, in global capture production in marine fishing areas (FAO, 2017). Most of the articles concerning these groups targeted commercial species such as anchovy and jack fish, and abalone and clams. A third group of importance in modelling were mammals (*N* = 48), which are among the most threatened species, facing severe population declines (Reeves et al., 2013), mainly owing to bycatch fisheries and pollution (Schipper et al., 2008), as well as ship strikes and noise disturbance (Aguilar de Soto et al., 2016; Pirotta et al., 2019), which now are recognized as major threats to marine mammals; hence, they are attractive for this kind of study. Another reason that makes these three groups suitable for modelling is the amount of data available. *Via* the OBIS portal (http://www.iobis.org/), > 20 million records are available for Pisces, > 3 million for Mollusca, and > 1 million for Mammalia. Other taxonomic groups well represented among the articles reviewed here were seaweed (*N* = 34), crustaceans (*N* = 29), seabirds (*N* = 28), and stony corals (*N* = 25). For seaweed, target species were mainly invasive, and crustacean included several economically important groups such as lobsters. Seabirds had a special interest for conservation, as well as stony corals since their ecological importance like habitat forming species.

Seagrasses are among the least studied groups (*N* = 10), even though they provide key ecological services, and there is a growing need for protection and conservation in the face of global threats (Orth et al., 2006). Two studies predicted the potential distribution and habitat suitability for the seagrasses *Zostera noltii* and *Z. marina* (Valle et al., 2011; Downie et al., 2013), yet we found just one article evaluating the impact of rising seawater temperatures and sea level rise on the distribution of *Z. noltii* (Valle et al., 2014). Other important habitat forming species that have received little attention are kelp forests and algae, but apparently they are receiving more attention since we found recent publications regarding kelp forests (Assis et al., 2018, 2017a), algae forest from the genus *Cystoseira* (Buonomo et al., 2018), and for the seagrass *Cymodocea nodosa* and *Posidonia oceanica* (Chefaoui et al., 2018; Chefaoui and Serrão, 2017). Other poorly represented groups were sponges, foraminifera, reptiles (*N* = 9 each), tunicates (*N* = 7), and bacteria (*N* = 2). Something worth mentioning is that we did not find articles regarding the study of viruses during years for which we conducted our review; however, a more recent article applies ENM to study the ecology and epidemiology of viral hemorrhagic septicemia virus of fish (Escobar et al., 2018). The study of marine diseases was less represented in the analyzed articles, nevertheless we think that distribution and niche models can help to better understand the complicated dynamic of epidemiological and diseases' processes in the marine realm.

In the category "reptiles" only turtles were found in the literature reviewed, which reflects the paucity of marine reptiles in comparison with fishes, but reptiles are probably receiving more attention since the recent publication of an article on niche modelling of sea kraits (Gherghel et al., 2018). "Other cnidarians" includes jellyfishes, anemones, black and red corals, the class Hydrozoa, and the extinct coral *Grewingkia*; all of these groups were much less represented in the literature. "Other invertebrates" includes the phyla Bryozoa, Placozoa, Entoprocta, Nematoda, Platyhelminthes, and Xenacoelomorpha; the
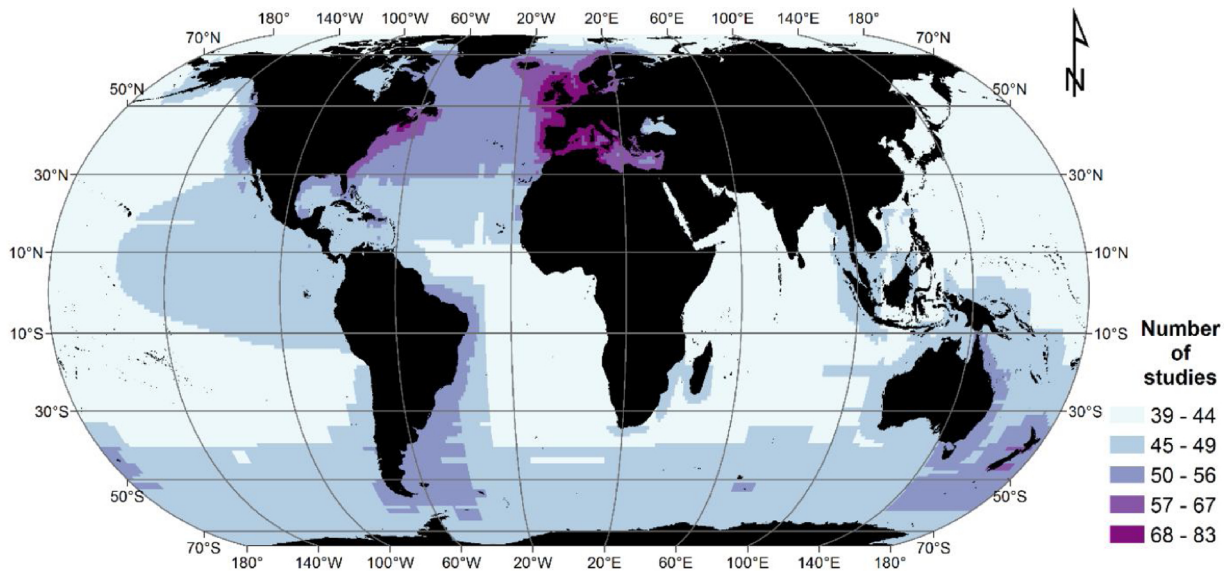
Fig. 3. Distribution of ENMs and SDMs studies worldwide taken from the 328 articles published between 1990 and 2016.
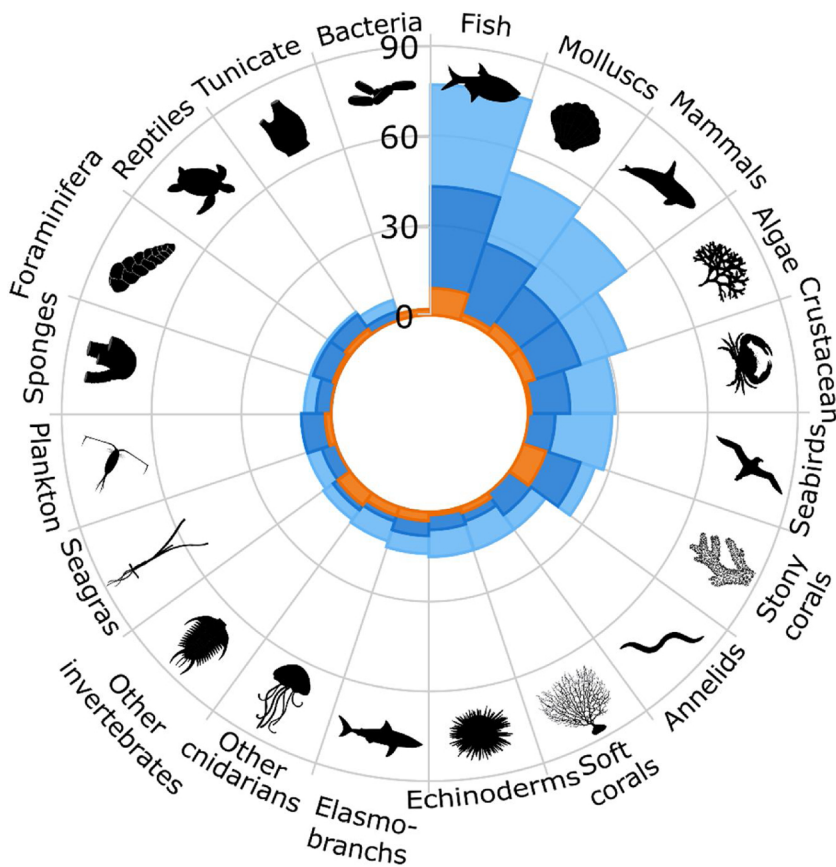

Fig. 4. Number of studies by taxonomic group of target species and extent of the study area. Numerous studies included more than one taxonomic group. Light blue, local studies; dark blue, regional studies; orange, global studies. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

class Priapulida; and the extinct class Trilobita. Many articles ($N = 50$) included multiple taxonomic groups.

4.3. Spatial patterns by taxonomic group

We found a strong interest in fish, molluscs, crustaceans, annelids, seaweed and sea grasses in western Europe and Mediterranean Sea (Fig. 5, Fig. B1 in Appendix B). Elasmobranch studies were more common in the Gulf of Mexico and near the United Kingdom; plankton studies were concentrated in the North Atlantic Ocean, mammals in the eastern Pacific Ocean, and echinoderms in the southwestern Pacific Ocean. Studies of seabirds were spread more globally, but with a marked interest in the Southern Ocean.

4.4. Occurrence data for modelling

One of the most important inputs for model construction is occurrence data, which provide information about environmental conditions where the species is present and thereby allow estimation of niches *via* correlative methods. The occurrence data used in the reviewed
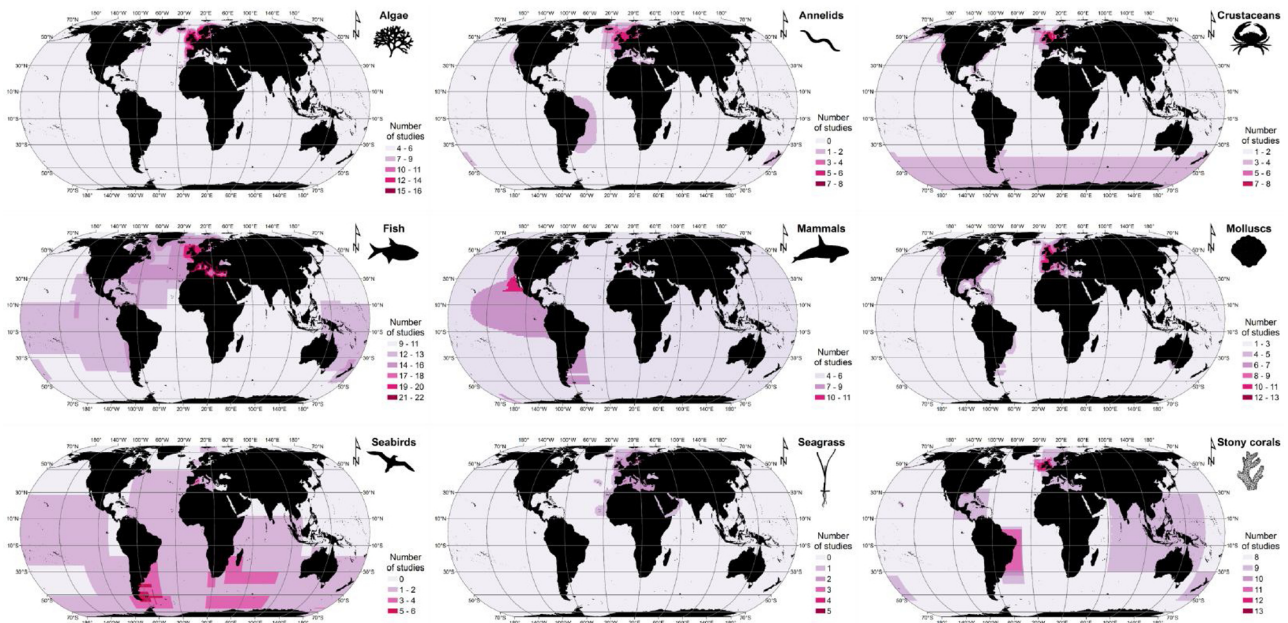
Fig. 5. Distribution of ENMs and SDMs studies per taxonomic group. For the other taxonomic groups see Fig. B1 in Appendix B.
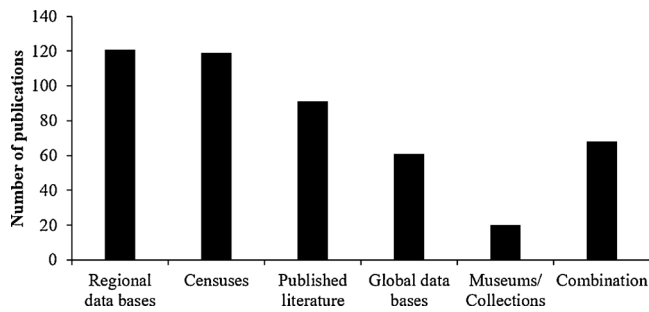

Fig. 6. Tendency in the use of species occurrence data sources.

literature (Fig. 6) most commonly came from regional databases (*N* = 121) and field censuses (*N* = 119). Other sources included published literature (*N* = 91), global databases (*N* = 61) and scientific collections (*N* = 20). It was relatively common for studies to combine different sources, especially for poorly-known species. Global initiatives that provide open access to occurrence data include the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/), Ocean Biogeographic Information System (OBIS, http://www.iobis.org/), FishBase (https://www.fishbase.de/), Fishnet2 (http://www.fishnet2.net/), and D4Science infrastructure (https://www.d4science.org/home). Other data sources are more specialized in particular taxa, such as the Microbis database from the International Census of Marine Microbes (ICoMM, https://vamps.mbl.edu/portals/icomm/icomm.php/microbis/) and the Global Diatom Database (Leblanc et al., 2012).

Example of regional efforts to compile accessible information on occurrences is the Continuous Plankton Recorder survey (CPR, https://www.cprsurvey.org/), in association with the Marine Biological Association of the UK, which holds historical data about biogeography and ecology of plankton from the North Atlantic and the North Sea (Helaouët and Beaugrand, 2009; Chust et al., 2014; Barton et al., 2016; Brun et al., 2016). Another example is the North Atlantic Right Whale Consortium (https://www.narwc.org/) that records historical sightings of right whales and other mammals, sea turtles, and large fish from the North Atlantic Ocean (Gowan and Ortega-Ortiz, 2014).

Alternative regional sources of occurrence data include commercial or recreational fisheries logbooks (Brodie et al., 2015; Gomez et al., 2015) and programs for assessment of fishing activity and stock

conditions (Maxwell et al., 2009; Tanaka and Chen, 2016). Among the latter, the International Bottom Trawl Survey in the Mediterranean (MEDITS, http://jadran.izor.hr/eng/international/medits.html) is a program that conducts continuous trawl surveys to assess the status of fishing resources, to support the policies and regulation of fisheries in the Mediterranean. Such data, besides providing information about occurrences, may also inform about their relative abundance, and thereby enable models aimed at studying effects of climate change on fish stocks. For instance, researchers have applied generalized linear and additive models to integrate swordfish *Xiphias gladius* and common sardine *Strangomera bentincki* fisheries data with simulations of future sea surface temperatures, to predict changes in their relative abundance and distribution off the coast of Chile (Silva et al., 2015).

Censuses were the second most common source occurrence data. Since most studies were at local scales, researchers can generate their own data. We found a variety of survey methods, including visual surveys (Pittman et al., 2007; Assis et al., 2015) and underwater video systems, especially for demersal species (Moore et al., 2009, 2016; Monk et al., 2010; McLean et al., 2016). Another common source was satellite tracking data, commonly used for sea turtles (Pikesley et al., 2015; Varo-Cruz et al., 2016; Whittock et al., 2016), seabirds (Skov et al., 2008; Catry et al., 2013; Ramos et al., 2015), and mammals (Edrén et al., 2010).

Information from natural history museums and scientific collections is another valuable source of primary data. Examples include the South Australian Museum (http://www.samuseum.sa.gov.au/collections; Bentlage et al., 2009), Museo Nacional de Historia Natural at Montevideo, Uruguay (http://www.mnhn.gub.uy/innovaportal/v/3090/12/mecweb/colecciones?leftmenuid=3090; Carranza et al., 2011), and the U.S. National Museum of Natural History (https://naturalhistory.si.edu/rc/; Georgian et al., 2014).

Occurrence databases frequently include important geographic biases, such as inaccurate geolocation and spatial autocorrelation among occurrence points, as well as species misidentifications. As with terrestrial ecosystems, it is common that certain marine areas are more visited than others because of their proximity or low-cost accessibility, which results in oversampling biases that turn into biases in the ecological niche space (Araújo and Guisan, 2006; also see Fig. 2). All modelling algorithms assume that occurrence data are unbiased (Araújo and Guisan, 2006), yet in reality they are sensitive to many

characteristics of the occurrence data (Araújo and Guisan, 2006; Loiselle et al., 2008; Fourcade et al., 2014). These biases can lead to model overfitting to environmental conditions associated with particular geographic spaces producing poorly reliable models (Araújo and Guisan, 2006; Boria et al., 2014), and also, impact model evaluation since in most cases there is no independent data to perform the test. A common practice is to randomly split occurrence data into training and testing subsets, despite both subsets keep sharing the same bias and may show an inflated metric for validation (Veloz, 2009). These remarks regarding biases and other problems associated to species occurrences are particularly important for pelagic and deep-water species that are hard to sample and, consequently, data-poor. Users and designers of occurrences databases must be aware of errors associated with this type of data acknowledging potential impacts on model performance, while also submitting occurrence data to exhaustive procedure of data cleaning (Peterson et al., 2011), and ideally by making specific mentions about data quality in metadata files at the time of making the data available.

4.5. Environmental data for modelling

Recent technological developments have enabled access to increasing amounts of environmental information, derived from remotely sensed data at high spatial resolutions, through data interpolation, or from modelled data (as with many climate data products). We found four main sources of environmental information: global data bases providing environmental parameters for whole oceans; information generated by the authors through either field measurements or computational methods; regional databases; and, in some cases, published information (Fig. 7). Global databases were by far the most common (N = 239). Among data portals most frequently used were the National Aeronautics and Space Administration (NASA) and National Oceanic and Atmospheric Administration (NOAA). Other data were accessed through the Ocean Color Web (https://oceancolor.gsfc.nasa.gov/), Physical Oceanography Distributed Active Archive Center (PODAAC, https://podaac.jpl.nasa.gov/), National Centers for Environmental Information (https://www.ngdc.noaa.gov/), World Ocean Atlas (WOA; https://www.nodc.noaa.gov/OC5/indprod.html), International Comprehensive Ocean-Atmosphere Data Set (ICOADS, http://icoads.noaa.gov/), AquaMaps (Kaschner et al., 2006; http://www.aquamaps.org/main/envt_data.php), MARSPEC (Sbrocco and Barber, 2013), GMED (http://gmed.auckland.ac.nz/), Bio-ORACLE (http://www.bio-oracle.org/), and The Copernicus Marine Environment Monitoring Service (CMEMS, https://www.copernicus.eu/en/services/marine), which is managed by the European Commission and offers products describing the physical and biogeochemical state of the global ocean and European regional seas. The most cited source for bathymetric data was the General Bathymetric Chart of the Oceans (GEBCO, https://www.gebco.net/), which offers a 15 arc-second resolution grid for the global ocean.

An example of a regional database is the Australian Bureau of Meteorology, consulted by Adams et al. (2015) to obtain data on wind speed and direction and solar exposure, with the goal of identifying environmental factors limiting seagrass survival in Moreton Bay,

Fig. 7. Tendency in the use of environmental descriptors for ENM and SDM.

Australia. Sarà et al. (2013) used hourly seawater temperature data from the Italian Oceanographic Buoy Network at the Instituto Superiore per la Protezione e la Ricerca Ambientale to generate a mechanistic model of fitness and potential colonization areas for the invasive mussel *Brachidontes pharaonis* in the Italian portion of the Mediterranean. Finally, Carlucci et al. (2016) used bathymetric data from the European Marine Observation and Data Network (EMODnet, http://www.emodnet.eu/what-emodnet) to assess driving forces influencing the distribution of dolphin species in the Gulf of Taranto. Generation of environmental variables by the authors themselves was not common; however, one example is the use of multibeam echosounder systems to produce bathymetric data (Howell et al., 2011; Monk et al., 2011; González-Irusta et al., 2015; Piechaud et al., 2015).

Selection of key environmental variables in which to explore the niche of species is a crucial step in model design. Inclusion of too many environmental dimensions can cause model overfitting (Peterson et al., 2007); thus, as good practice, various biological or statistical criteria are used to select the best set of environmental predictors. Principal components analysis (PCA) is the most commonly used to reduce dimensionality of environmental spaces (Dennis and Hellberg, 2010; Freeman et al., 2013; Escobar et al., 2015). Another common procedure for variable selection involves the estimation of correlation among candidate variables, combined with the results of a jackknife analysis performed in Maxent; under this method, variable selection obeys low collinearity and high contribution values (Raghavan et al., 2019a,b).

In marine environments, the water column creates a three-dimensional structure that represents an extra challenge in modelling (Dambach and Rödder, 2011; Robinson et al., 2011). The study of pelagic organisms represents a particular challenge given the difficulties of access and sampling in open oceans (Bentlage et al., 2013). Most oceanographic data are representative of the topmost layers of the water column, and those representative of the seabed are often derived from bathymetric profiles (Assis et al., 2017a), which impedes modelling of pelagic and highly mobile species. Bentlage et al. (2013) modelled the potential distribution of the open-ocean jellyfish *Periphylla periphylla* on a global scale, they used oceanographic variables (WOA05) at multiple depths, and added the third dimension by transforming and combining all depth layers into a single, continuous, grid two-dimensional that replicated global oceans multiple times. As such, the model encompassed the whole environmental range occupied by the species in three dimensions. Duffy and Chown (2017) used similar approaches to estimate the probability of occurrence of four fish species in the northeastern Atlantic, highlighting the importance of explicit consideration of the vertical dimension.

The temporal resolution of environmental layers is important, especially in the case of highly mobile species, since their distributions may be associated with both short- and long-term variability in ocean environments (Fernandez et al., 2017; Mannocci et al., 2017). In the literature reviewed here, little attention was paid to this point, and the use of variables appeared more related to availability than to detailed analysis of impacts of temporal resolution on distributions of target species. An exception is the work of Scales et al. (2016), who used remotely-sensed environmental variables that temporally matched with tracking data for the Grey-headed Albatross *Thalassarche chrysostoma* to identify foraging areas. Fortunately, it seems that this field is gaining attention among the modelling community since contributions addressing this topic, although mainly focusing on mammals, have been recently published. It has been found that finer temporal scales may provide more accurate models, especially for species such as blue, fin and sei whales that are highly dependent on dynamic variables (Fernandez et al., 2018). Other studies regarding the spatio-temporal variability and habitat dynamism for modelling the distribution of blue whales in the Azores islands and the California coast in USA highlighted the utility of multiscale studies to capture the factors that affect the distribution of this highly migratory species (Abrahms et al., 2019; González-García et al., 2018); these contributions have been important
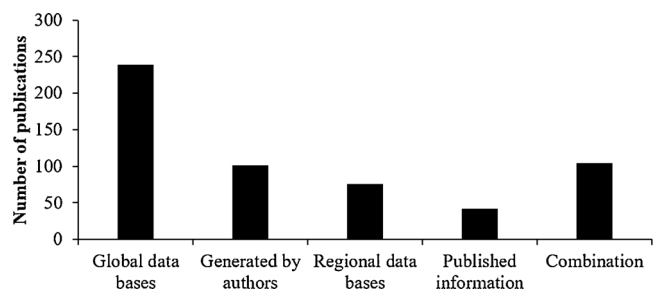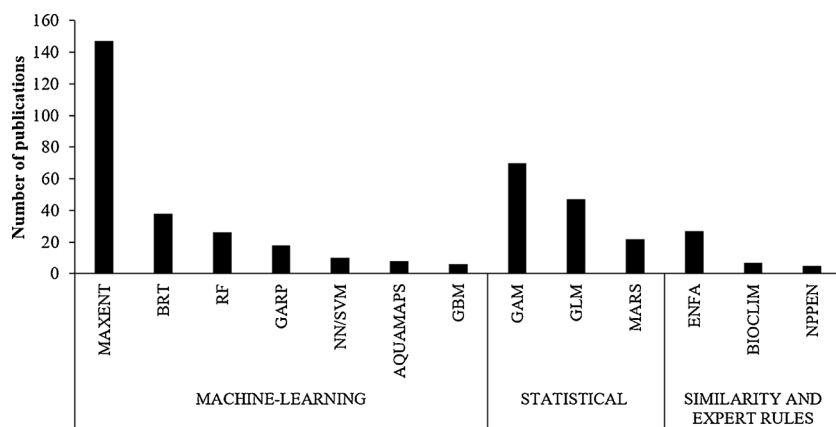
Fig. 8. Tendency in the use of ENM and SDM algorithms. We present only the most frequently used algoritms. MAXENT = Maximum Entropy; BRT = Boosted Regression Trees; RF = Random Forest; GARP = Genetic Algorithm for Rule Set Production; NN/SVM = Neural Networks/Support Vector Machine; GBM = Generalized Boosting Models; GAM = Generalised Additive Model; GLM = Generalized Linear Model; MARS = Multivariate Adaptive Regresion Splines; ENFA = Ecological Niche Factor Analysis; NPPEN = Non Parametric Probabilistic Ecological Niche.

to understand how species make use of, or shift among, dynamic habitats and to reinforce the importance of such models for conservation strategies.

Influences of data quality on model performance have been investigated for marine systems. Becker et al. (2016) compared the performance of two cetacean density models, one built with oceanographic information and the other with data measured *in situ*; they found no significant differences in the metrics evaluated, suggesting that modelled data, which are considerably easier and less costly to assemble, can support modelling efforts adequately. To assess effects of spatial resolution on model predictions, Basher et al. (2014) modelled distributions of shrimp species in the Ross Sea; they found that spatial resolution influences both the extent of the resulting suitable area, and the relative importance of environmental variables.

A great diversity of variables was used to describe species' niches, including physical and chemical properties of the water column, topographic characteristics of the seabed, factors describing the surrounding environments, and variables related to biotic interactions (Table C1, Appendix C). The most common descriptor used was water temperature, which was used in 240 of the articles reviewed. Temperature is among the most important determinants of species' distributions, and as a single environmental covariate can predict 53–99 % of present-day biogeographic units along coastlines (Belanger et al., 2012). Other physical variables included photosynthetically active radiation (PAR, $N = 26$) and diffuse attenuation coefficient ($N = 20$); chemical variables included salinity ($N = 147$) and chlorophyll-*a* concentration ($N = 97$); atmospheric variables included air temperature ($N = 15$) and precipitation ($N = 9$); environmental descriptors included sediment type ($N = 30$) and substrate/bottom type ($N = 27$); geographic variables included distance to shore ($N = 54$) and geographic coordinates ($N = 20$); hydrodynamic variables included current velocity ($N = 45$) and mixed layer depth ($N = 15$); topographic variables included bathymetry ($N = 210$) and slope ($N = 109$), ecological variables included habitat type ($N = 11$) and presence/absence/biomass of other species ($N = 7$); finally, temporal variables included season of the year ($N = 7$) and calendar year ($N = 4$).

4.6. Model types

4.6.1. Correlative models

Correlative modelling was far more frequent than mechanistic or process-oriented approaches. It usually begins with the known distribution of species, namely presence, presence-absence or abundance data, which are associated statistically with environmental variables describing dimensions such as climate (Kearney, 2006; Peterson et al., 2015). Its popularity is thanks partly to advances in statistical techniques, development of GIS tools, and availability of specialized modelling software, and also to growing availability of detailed data about biodiversity and the environment (Elith and Leathwick, 2009; Peterson

et al., 2015). In our review, 307 of the articles were exclusively correlative associations, so the general tendencies described above represent the main currents in correlative modelling in largest part. Thus, the main focus of this section is on description of methods used in correlative models.

Models differ in the way they select environmental predictors and measure variable contributions and predictive performance (Elith et al., 2006), but they have in common the goal of describing one part of environmental space as suitable, and the rest of that space as unsuitable. In the earliest marine models, Reilly (1990) applied analysis of variance to explore relationships between water mass properties (density and thermocline depth) and seasonal distributions of dolphin groups in the eastern tropical Pacific. Fiedler and Reilly (1994) and Reilly and Fiedler (1994) used canonical correspondence analysis (CCA) to study, respectively, habitat use and the relationship of dolphin abundance to habitat quality. More recently, a great variety of methods has been used for modelling species niches and distributions (Franklin, 2009). In our review, most popular methods were machine-learning methods ($N = 268$), followed by statistical methods ($N = 189$), and finally similarity-based and expert-rule approaches ($N = 54$); 74 studies used a combination of two or more techniques. Among machine-learning methods, Maxent (Phillips et al., 2006) was most frequent ($N = 147$; Fig. 8). Since the appearance of Maxent in 2006, it became one of the most popular modelling techniques, perhaps partly because it requires relatively little information, being designed to work with presence-only data (Phillips et al., 2006). Maxent has shown robust predictive accuracy (Elith et al., 2006; Graham et al., 2008) even with small sample sizes (Hernandez et al., 2006; Wisz et al., 2008), and provides great flexibility in model construction through a friendly interface (*e.g.* features and regularization multiplier) that allow the user to adjust the model to specific needs and available information (Merow et al., 2013; Muscarella et al., 2014). Other well-represented machine-learning methods have been boosted regression trees (BRT, $N = 38$) and random forests (RF, $N = 26$). In the case of statistical methods, most frequent were regression models (*i.e.* GAMs, $N = 70$ and GLMs, $N = 47$; Fig. 8). Among similarity-based and expert-rule models, most frequent was the ecological niche factor analysis (ENFA, $N = 27$; Fig. 8). In spite of their applicability and overall quality or popularity in the field of correlative modelling, it is has been recognized that there is no single "best" algorithm, and it is recommended, as a good practice, to test and justify a suit of algorithms in order to choose the best option for a particular research question (Qiao et al., 2015).

4.6.2. Mechanistic models

Mechanistic models use detailed physiological information and first-principles of mathematical reasoning to determine links between the environment and the fitness of the organism, which is later represented in geographic space (Kearney, 2006; Kearney and Porter, 2009; Peterson et al., 2015). In our review, only 13 articles used mechanistic

approaches. Dynamic energy budget (DEB) models used chlorophyll-a to express food availability, and water temperature to express body temperature, to study relative fitness of native and invasive molluscs; this approach generated spatial predictions of their physiological performance and highlighted potential areas for colonization (Sarà et al., 2013; Montalto et al., 2015). Mechanistic niche models have been used to integrate solar radiation, salinity, and temperature in models designed to evaluate the invasive potential of the ascidian *Ciona intestinalis* and the seaweed *Codium fragile* (Madariaga et al., 2014). Other studies have assessed future changes in distributions of planktonic organisms in response to rising temperatures (Helaouët and Beaugrand, 2009; Thomas et al., 2012).

Other mechanistic niche models explicitly incorporate correlative approaches. For instance, Fordham et al. (2013a, 2013b) modelled the future ranges and abundance of two harvested abalone species (*Haliotis rubra* and *H. laevigata*), combining demographic processes and physiological responses with climatic factors. Other studies have used thermal thresholds of macroalgae to predict potential range shifts in response to global warming (Martínez et al., 2014), or have simulated effects of temperature and oxygen concentrations on growth and body weight in fish and invertebrates to predict patterns of change in species richness, invasion, and extinction worldwide (Jones and Cheung, 2014). For two ecologically and economically important mussels, *Mytilus edulis* and *M. galloprovincialis,* energetic responses to temperature were analysed to understand current and future potential distributions (Fly et al., 2015).

4.6.3. Process-oriented models

Dynamic models can take into account key processes that affect ranges of species through effects on demographic processes such as birth and death rates, and dispersal of individuals (Case et al., 2005; Holt and Keitt, 2005). Process-oriented models can measure effects of these processes across species' distributions (Peterson et al., 2015). In this review, only five of the articles included process-oriented modelling, almost all focused on molluscs and related to their dispersal capabilities.

Process-oriented models can be combined with correlative approaches. Among the articles reviewed, the earliest process-oriented model (Inglis et al., 2006) examined the utility of habitat suitability index models and particle dispersion models to project suitable habitat for the non-native bivalves *Theora lubrica* and *Musculista senhousia* in New Zealand. For *M. galloprovincialis,* which is invasive in southern Africa, Assis et al. (2015) combined niche modelling and Lagrangian particle simulations to assess its current distribution and evaluate effects of dispersal capacity and environment as controls on its potential to spread. In the Bay of Santander, Spain, Bidegain et al. (2013) combined niche modelling with a particle-tracking model to study larval transport, supply, settlement behavior and post-settlement mortality of the clams *Ruditapes decussatus* and *R. philippinarum*, to identify optimal habitat for settlement and assess connectivity between spawning and nursery grounds. Finally, Elsäßer et al. (2013) combined niche and particle dispersal models to identify suitable areas for adult translocation that could represent restoration sites for biogenic reefs formed by the horse mussel *Modiolus modiolus* in Northern Ireland. In our only example including fish, Cheung et al. (2009) analysed likely effects of climate change on distributions of 1066 commercially exploited marine fish and invertebrates using a dynamic model including environmental variables and simulations of abundances derived from a logistic population growth model.

4.7. Model selection and validation

Model selection and validation is a critical step in the model procedure, it is the measure of how useful and trustworthy our models are, most importantly when the intention is transferring the model to novel conditions (Wenger and Olden, 2012). Considering only correlative models, 224 articles used a cross-validation method, mostly by randomly dividing occurrence data, whereas only 21 used independent test data. The most frequent evaluation measure was the threshold-independent area under the receiver operating characteristic (ROC) curve (AUC; $N = 177$), followed by the Akaike´s information criterion (AIC or AICc; $N = 42$), the true skill statistics (TSS; $N = 35$) and the Kappa statistic ($N = 26$); 111 articles combined more than one validation metrics.

Model selection is a debated topic in ENM and SDM currently (Warren and Seifert, 2011), and newer applications that run Maxent and other algorithms have adopted statistical model evaluations and metrics based on information criteria as the standard to choose among all possible combinations of model parameterizations (Muscarella et al., 2014; Cobos et al., 2019). Such approximations to model selection and evaluation represent a more robust protocol while implementing ENM, and have demonstrated to yield better results than only using default parameters.

4.8. ENMs and SDMs applications

4.8.1. Current species distribution patterns

Models are often used to investigate factors that limit species' distributions, and to fill gaps in information about species' ranges. In our review, 212 of the articles aimed to explore potential distributions of species or to elucidate which environmental factors are responsible for observed patterns. Most distributional studies concerned fish, mammals, molluscs, or seaweed (Table 1). For instance, ENM and SDM have been used to investigate the potential distribution of the harmful cyanobacteria *Lyngbya majuscula* in the Canary Islands (Martín-García et al., 2014), and to measure the effect of environmental variables on shaping the distribution of fish species (Beger and Possingham, 2008; Chatfield et al., 2010), for the kelp *Laminaria hyperborea* (Assis et al., 2016b), and for commercial cephalopods (Lauria et al., 2015). For several articles, a study of the distribution patterns was the first step toward answering more complex questions including topics such as climate change impacts and conservation planning.

4.8.2. Impacts of future climate change

The average global surface temperature of the Earth has increased by approximately 0.2 °C per decade over the past 30 years (Hansen et al., 2006). More than 90 % of the excess heat is absorbed by the ocean, driving to a rate of warming of about 0.11 °C per decade in the upper layer, and an increase in the global mean sea level of 0.19 m and a decrease of seawater pH by 0.1 units in recent decades (Rhein et al., 2013). Of the articles reviewed, 64 aimed to analyse some aspect of future climate change; the most frequent taxa in these studies were fish and molluscs (Table 1). Model scenarios have been used to improve understanding of how climate change may impact marine ecosystems and species; most have focused on predicting potential changes of species' distributions in response to climate change.

For example, Assis et al. (2016b) used niche modelling to predict consequences of future climate change on the distribution and genetic diversity of the kelp *L. hyperborea* in Europe. They suggested that changes in environmental conditions may lead to loss of suitability in areas where the species has persisted through time, and a possible northward range shift. A model of shallow coral reefs worldwide (Couce et al., 2013) assessed potential effects of increasing sea surface temperature and ocean acidification on these ecosystems; temperature would be the main driver in the decline of suitability, particularly in the Indo-Pacific region, and in producing a poleward range expansion of suitable areas.

4.8.3. Methodological advances

In the past two decades, use of models has grown rapidly (Lobo et al., 2010), with a concomitant increase in interest in improving their performance. Of the 328 articles reviewed here, however, only 41 addressed performance of the models. The most frequent way to evaluate

Table 1

Total number of articles and percentage by taxonomic group and application. For the purpose of this review elasmobranch are taken as a separate group from the category fish. Numbers are calculated considering only articles evaluating some aspect of a taxonomic group (324 in total), this excludes review articles. An article was counted more than once if two or more taxonomic groups or applications were modelled in a single study.

	Distribution	Climate change	Method evaluation	Conservation planning	Range shifts	Invasive species	Properties of populations and communities	Past climates	Other applications
N	212	63	41	36	31	32	31	18	14
Annelids	6	3	2	1		3		1	1
Bacteria	2	1							1
Crustaceans	10	6	5	2	1	6		3	1
Echinoderms	7	3	3	1		1	1	1	2
Elasmobranchs	9	4	1	2	2		1	1	1
Fish	37	16	13	9	6	6	11	3	2
Foraminifera	6	4	1	1		2		1	
Mammals	30	3	6	7	10		9	1	2
Molluscs	25	13	5	9		8	5	4	5
Other cnidarians	7	2	2	1					1
Other invertebrates	5	3	2						2
Plankton	4	6	1		1	1	2		1
Reptiles	6	4							
Seabirds	15	3	3	7	11			1	2
Seagrass	7	2	3	2					
Seaweed	21	9	4	1		11	2	4	1
Soft corals	12	5	5	3					1
Sponges	6	2	1	3					
Stony corals	15	7	3	1		3		1	1
Tunicates		1				6			

performance was to compare the results of multiple techniques in a single scenario. For instance, Jones et al. (2012) compared the performance of three different approaches, AquaMaps, Maxent, and Sea Around Us Project algorithms in modelling commercial fish distribution in the North Sea and North Atlantic. Bucas et al. (2013) compared outcomes of four modelling algorithms: GAMs, RF, MARS, and Maxent, in predicting the distribution and diversity of benthic species in the Baltic Sea.

Another contribution to methodological advance is ensemble modelling approaches; that is, results from different algorithms can be combined to produce a more robust model, including results from more than one set of model parameters (Thuiller et al., 2009). In the marine realm, ensemble models have been used to predict potential distributions of flatback turtles *Natator depressus* (Whittock et al., 2016), future suitability for the Barau's Petrel (*Pterodroma baraui*; Legrand et al., 2016), and impacts of climate change on fish diversity in the Mediterranean Sea (Albouy et al., 2015).

Other authors have evaluated transfer capability of models; for example, Lauria et al. (2015) evaluated model capacity to spatially predict density of the commercially important Norway lobster *Nephrops norvegicus* in fishing areas of the Northeast Atlantic; they found that most of the models were able to successfully predict lobster density among fishing areas, suggesting that simple regression models perform as well as complex models in space transferability. Verbruggen et al. (2013) studied the model transfer capability for the invasive seaweed *Caulerpa cylindracea*, they found that appropriate predictor selection plays an important role in transferability success. Projection exercises are a difficult task in the field of modelling because we don't have the capacity to validate that a successful model predicting the actual distribution of species is equally successful in predicting its distribution on novel conditions when projected to new areas or in climate change scenarios. It has been shown that when transferring models it is difficult to accurately estimate the existing fundamental niche of species, specially when it is not well represented in the calibration area (Qiao et al., 2019). It is also of high importance to evaluate the degree of environmental similarity between calibration and projection regions, as well as to make a proper selection of the modelling algorithm considering the completeness in the knowledge of the species fundamental niche (Qiao et al., 2019). Despite this, model projections represent a valuable tool to explore phenomena such as invasive species (Jiménez-Valverde et al.,

2011) or climate change impacts (Pearson and Dawson, 2003).

Implementation of new modelling methods represents efforts to improve ENM and SDM capabilities. For instance, Ready et al. (2010) presented the online approach AquaMaps (http://www.aquamaps.org), designed to estimate suitability for species on the basis of presence-only data and a set of environmental variables, while incorporating expert knowledge to account for potential bias in data sets. The performance of AquaMaps models have been found to compare well with other methods such as Maxent and GLM (Ready et al., 2010). Johnston and Purkis (2012) developed Invasionsoft, a web-based modelling tool designed to study marine invasions using a cellular automata algorithm to relate historical records of the invasion process of the species of interest with a set of environmental descriptors. In a test case using lionfish and seaweed, the algorithm was able to emulate the spread of those marine organisms, nevertheless we are not aware of other articles using this software.

4.8.4. Conservation planning

Conservation management can benefit from models that provide information about present-day distributions (Galparsoro et al., 2009), range shifts expected under climate change (Chust et al., 2014), potential spread of invasive species (De Rivera et al., 2011), and habitat use (Ballard et al., 2012; La Manna et al., 2016). Of the 328 articles reviewed, 36 included some aspect of conservation planning, most commonly for fish, molluscs, mammals, and seabirds. The most common goal was to designate marine protected areas (MPAs); for example, Ballard et al. (2012) combined ENMs of whales, seals, and seabirds along with information on their feeding habits, to identify sites in the Ross Sea most important for conservation. Similar studies have been conducted for marine mammals in Scotland (Embling et al., 2010), fish in New Zealand (Leathwick et al., 2008), and kelps in France (Bajjouk et al., 2015). Models have also been used to identify sites of vulnerability to pollution in seabirds (Lieske et al., 2014), vulnerability to fishing mortality for commercial species (Abecasis et al., 2014), and potential risk of bycatch for marine mammals (Briscoe et al., 2014).

4.8.5. Range shifts

Animal populations tend to move or shift their geographic ranges in response to specific conditions across marine habitats. These conditions may vary through the life history of a single organism, such as in

seeking predator-free sites, or optimal sites for feeding or spawning (Afonso et al., 2014; Fromentin and Lopuszanski, 2014). Species' distributions in space and time reflect spatial patterns in population dynamics, an important issue in conservation, and particularly for migratory species that have complex spatial dynamics, since they may change habitat preferences between migratory endpoints or during different life-history stages (McKinney et al., 2012). Of the 328 articles reviewed, 31 were related to these issues, particularly in seabirds and mammals. For instance, some authors have tried to predict foraging sites dynamics for seabirds, including the albatrosses *Diomedea exulans* (Louzao et al., 2013) and *Thalassarche chrysostoma* (Scales et al., 2016), and the gannet *Morus bassanus* (Skov et al., 2008). Models have also been used to identify optimal chick-rearing habitats for *Pygoscelis* penguin species (Cimino et al., 2013). For mammals, models have been applied to identify habitat partitioning in humpback whales between different reproductive states and behaviors (Lindsay et al., 2016); other cases include modelling species' distributions among seasons (Reilly, 1990; Pitchford et al., 2016). For fish, models have been used to identify optimal sites for feeding, spawning, and nursery areas (Florin et al., 2009; Druon et al., 2015, 2016; González-Irusta and Wright, 2016).

4.8.6. Invasive species

Invasive species represent one of the main causes of biodiversity loss (Bellard et al., 2016); they can displace native species, change the community structure and function, and cause significant economic losses by affecting ecosystem services (Molnar et al., 2008; Pejchar and Mooney, 2009). Consequently, understanding and predicting the potential for spread of invasive exotic species is crucial to effective management. Applications of models to invasive species have sought to evaluate their potential to spread (also see section on Methodological advances above).

Of the 328 articles reviewed, 32 were related to invasive species, particularly on seaweed (Table 1). For example, researchers have used models to investigate the potential for spread and the environmental factors that favor or limit the establishment of species such as the invasive kelp *Undaria pinnatifida* at local (Báez et al., 2010) and global (James et al., 2015) scales, the mussel *Mytilus galloprovincialis* in southern Africa (Assis et al., 2015), the scleractinian corals *Tubastraea coccinea* and *T. Tagusensis* in Atlantic waters Carlos-Júnior et al., 2015a,b), and the seastar *Asterias amurensis* in the Southern Ocean (Byrne et al., 2016). In another example, niche models were built to test niche conservatism of fish in the Mediterranean Sea (Parravicini et al., 2015); this topic, has rarely been explored in marine organisms.

4.8.7. Properties of populations and communities

Herein, "properties" refers to abundance, biomass, density, and richness. Of the 328 articles reviewed, 31 focused on these subjects, with fish and mammals as the most frequent taxa (Table 1). The most common topic was prediction of species abundance. Within the 1990–2016 literature search, the earliest work we found that used statistical procedures to relate abundance to environmental variables (Fiedler and Reilly, 1994) combined cetacean sighting data with *in situ* data of temperature and thermocline depth and thickness *via* canonical correspondence analysis to calculate a habitat quality index. For fish, niche models have been used to predict relative abundance of the mesopelagic fish *Electrona antarctica* in the Southern Ocean (Loots et al., 2007) and the swordfish *Xiphias gladius* in the Indian Ocean (Lan et al., 2014), and to predict potential changes in abundance for *X. gladius* and the sardine *S. bentincki* in the Pacific under climate change (Silva et al., 2015). Other groups of interest in predicting abundances have been rays (Dedman et al., 2015) and molluscs with commercial importance, such as abalone (Russell et al., 2012; Fordham et al., 2013a).

Density and biomass have been estimated for fish populations in the Pacific (Su et al., 2011) and Atlantic oceans (Lynch et al., 2015) considering climate change predictions, and for mammals in the Pacific

Ocean (Becker et al., 2012, 2016). Knudby et al. (2011) used ENMs to predict species richness, diversity, and biomass of fish in the Fiji Archipelago. Other studies have modelled biomass of kelp species in France (Gorman et al., 2013; Bajjouk et al., 2015), detected biomass hot-spots of bivalves in the Baltic Sea (Darr et al., 2014), and modelled bivalve densities in the Mediterranean Sea (Vázquez-Luis et al., 2014). Models have estimated species richness for fish in the Caribbean (Pittman et al., 2007), and potential changes in mammalian species richness worldwide under climate change scenarios (Kaschner et al., 2011).

4.8.8. Modelling past distributions

The Earth's climate has experienced continuous changes over the past 65 million years and beyond, shifting from extreme warmth to extreme cold (Zachos et al., 2001). Past and current evidence suggests that changing climates profoundly influence expansion or contraction in species' ranges (Pearson and Dawson, 2003); knowledge of species' responses to past climatic changes helps to anticipate responses to future climate changes (Araújo and Pearson, 2005; Kettle et al., 2011). Models have been used to explore the biogeographic history of several marine species; 18 of the articles reviewed were related to past climates, focusing on seaweed, molluscs, crustaceans, fish and mammals (Table 1). For example, Saupe et al. (2015) used ENM to evaluate the vulnerability to extinction of 92 bivalve and gastropod species that lived during the mid-Pliocene Warm Period, by relating niche breadth, geographic range size, and area availability. For seaweed, models have been used to explore influences of past climates on the distribution and genetic composition of *Saccorhiza polyschides* (Assis et al., 2016a), *Laminaria hyperborea* (Assis et al., 2016b), and *Fucus vasiculosus* (Assis et al., 2014) populations. For marine fish, Last Glacial Maximum distributional patterns have been modelled (Bigg et al., 2008; Kettle et al., 2011).

4.8.9. Other applications

Finally, 14 of the articles reviewed used models to study other aspects of marine taxa such as the relationship between phylogenetic structure and distributional patterns of gastropod species (Carranza et al., 2011), to test for niche shifts in invasive coral species (Carlos-Júnior et al., 2015a), to understand evolutionary niche dynamics of seaweed (Verbruggen et al., 2009), to test long term niche stability of benthic species (Brame and Stigall, 2014), to study niche divergence among closely related seabirds in combination with stable isotope analysis (Rayner et al., 2016), and to compare realized ecological niches of phytoplankton species categorizations of populations strategies and functional groups (Brun et al., 2015).

4.9. Spatial patterns by application

We observed an emphasis in western Europe on the study of distributions in current, future, and past climate scenarios. Studies of invasive species were mostly in the Mediterranean Sea, which has had numerous biological invasions, mainly thanks to the Suez Canal, and also from aquaculture and the aquarium trade (Katsanevakis et al., 2014, 2016; Galil et al., 2015); a secondary focus of invasive species was on the Brazilian coast. Conservation planning was of particular concern in the United Kingdom. Most studies concerning conservation or management were across small areas, appropriate in the context of conservation efforts for which legal responsibility relies in local agencies (Boersma and Parrish, 1999). Studies related to habitat use were more uniformly distributed across all oceans (Fig. 9).

5. Concluding remarks

Our examination of the published literature revealed an enormous interest in application of ENMs and SDMs to explaining and predicting distributional patterns and the processes shaping them for marine
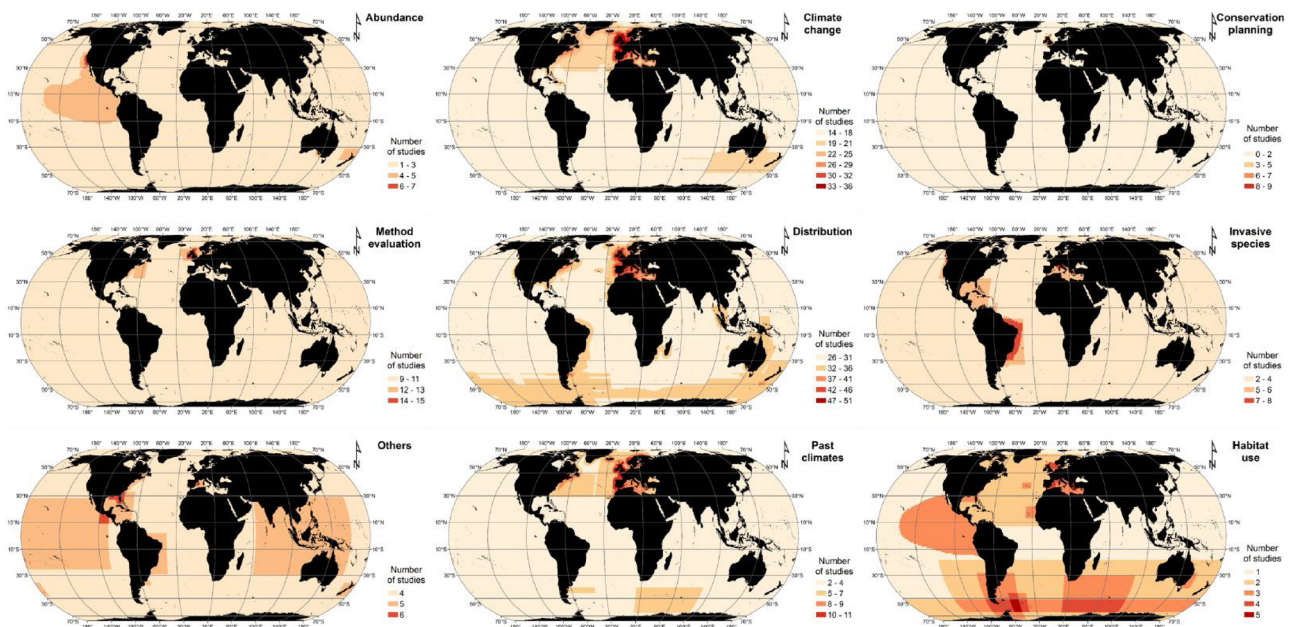
Fig. 9. Spatial distribution of ENMs and SDMs per model application.

species. The most common research questions are headed towards the understanding of the processes shaping species distributions and the impact of climate change on species habitat suitability and distribution. Taxonomic groups more studied are fish, molluscs and mammals, obeying the economic and ecological relevance of the first two, and conservation importance of the last. Taxonomic groups least represented are sponges, foraminifera, reptiles, tunicates and bacteria. We also found little representation of important habitat forming species such as shallow and deep scleractinian corals, kelp forests and seagrasses; even though recently have been published more studies about these groups, we think is of primer importance to keep addressing them in the research agenda in the face of growing threats to marine ecosystems.

A wide range of modelling techniques is available; the correlative approach is by far the most common, but mechanistic or process-oriented modelling approaches can be more appropriate in some cases, although are generally more difficult to implement given the amount and quality of data they require for proper calibration (*e.g.* physiological and demographic parameters, dispersal capacity). Mechanistic models, have the advantage that by incorporating physiological information have a stronger predictive power and thus, are more suitable in cases such as range shifts, climate change impacts or species invasions. Process-oriented models that include distribution potential and populations dynamics are adequate to predict species' distributions in spatially and temporally explicit frameworks, not only accounting for habitat suitability. As such we suggest strongly that choice of modelling technique follow the needs of the specific question and data availability.

Common problems and pitfalls rely on the lack of clarity in the concepts and on a proper use of ecological niche theory behind model design. Many articles do not differentiate clearly between ecological niche models and species distribution models. Proper use of these concepts is greatly encouraged, although, these issues are not exclusive to modelling in marine environments. Many articles failed to clarify the niche concepts used (*e.g.* fundamental, existing or realized niche) or the criteria used to define their modelling framework (*i.e.* the basis upon which the modelling technique was chosen). Many articles did not make clear that they had considered limitations of the data (occurrence

or environmental; *e.g.* spatial autocorrelation among occurrence points). We call for a rigorous process of model selection and validation in order to generate models as reliable as possible, specially when research questions go beyond theoretical interest, that is to say, with explicit interest in the application of models to conservation and management issues.

Unique aspects of marine modelling that impose and extra challenge are related to the dynamic nature of marine ecosystems. We highlight the need to understand and incorporate these complex dynamics especially in the case of highly mobile pelagic organisms by paying special attention to the temporal and spatial scales being handled in the models. The additions of a third dimension in representing the marine realm from a volumetric perspective has yet to be incorporated more broadly. These unique aspects of marine habitats urge to multidisciplinary work that help us to understand how the processes inherent to the ocean, influence species' distributions. Improved understanding of how niche theory and modelling approaches apply to marine environments will lead to the development of more realistic niche models, especially in the case of conservation planning, climate change, and impacts of invasive species, where they represent useful tools in decision-making. Also, it is of utmost importance to develop models that can be truly incorporated in real life solutions to conservation and management needs, as well as to bet for the combinations of this models with other fields such as evolution, trait-based approaches, or even social and legislative matters, which can guide us to a better understanding of ecosystems processes and species' responses to extant and novel environmental conditions.

Oceans cover more than 70 % of Earth's surface and around the 95 % of it remains unexplored. Many marine resources are considered as "goods" for human beings, and we obtain from them an important number of services. There is a strong bond between oceans and humanity, and an urgent need to understand de complex dynamic and processes occurring in order to protect, conserve or recover our ocean ecosystems. ENMs and SDMs represent a valuable tool for this research, but only when more clarity infuses study design and conception, including correct use of concepts, niche theory, aims and methodology, will niche modelling be fully able to enhance in the marine realms.

Author contributions

SMMM and HRB conceived the idea. SMMM performed literature search and analysis of information. ALN contributed to the formal analysis, visualization and interpretation of results. SMMM wrote the original draft and ALN contributed to review and edit the manuscript.

Declaration of Competing Interest

Authors declare no conflict of interest.

Appendix A. Bibliographic list of the 328 articles included in the review

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Appendix B
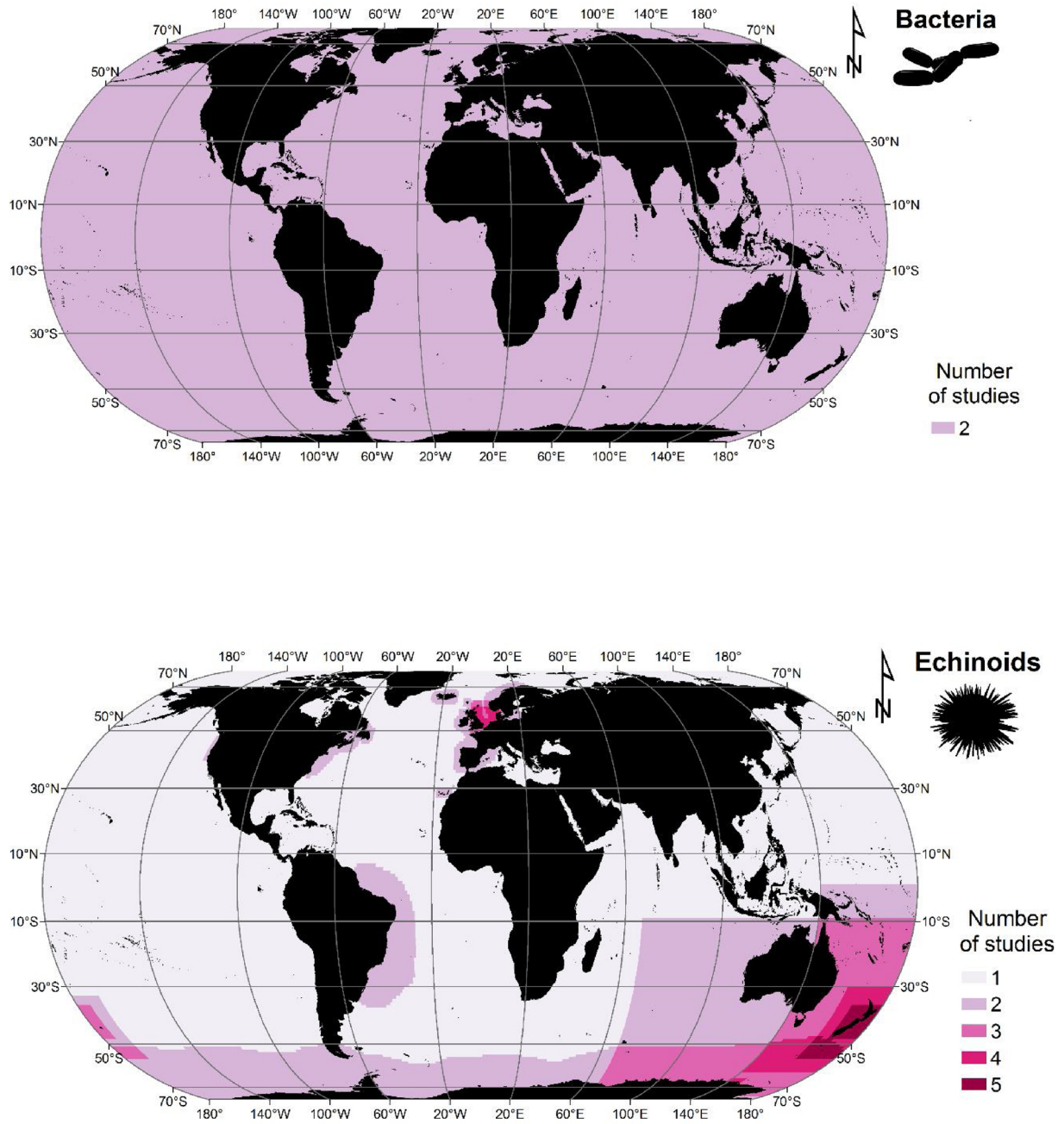
Fig. B1. Maps showing the spatial distribution of taxonomic groups not presented in the main text of the article.
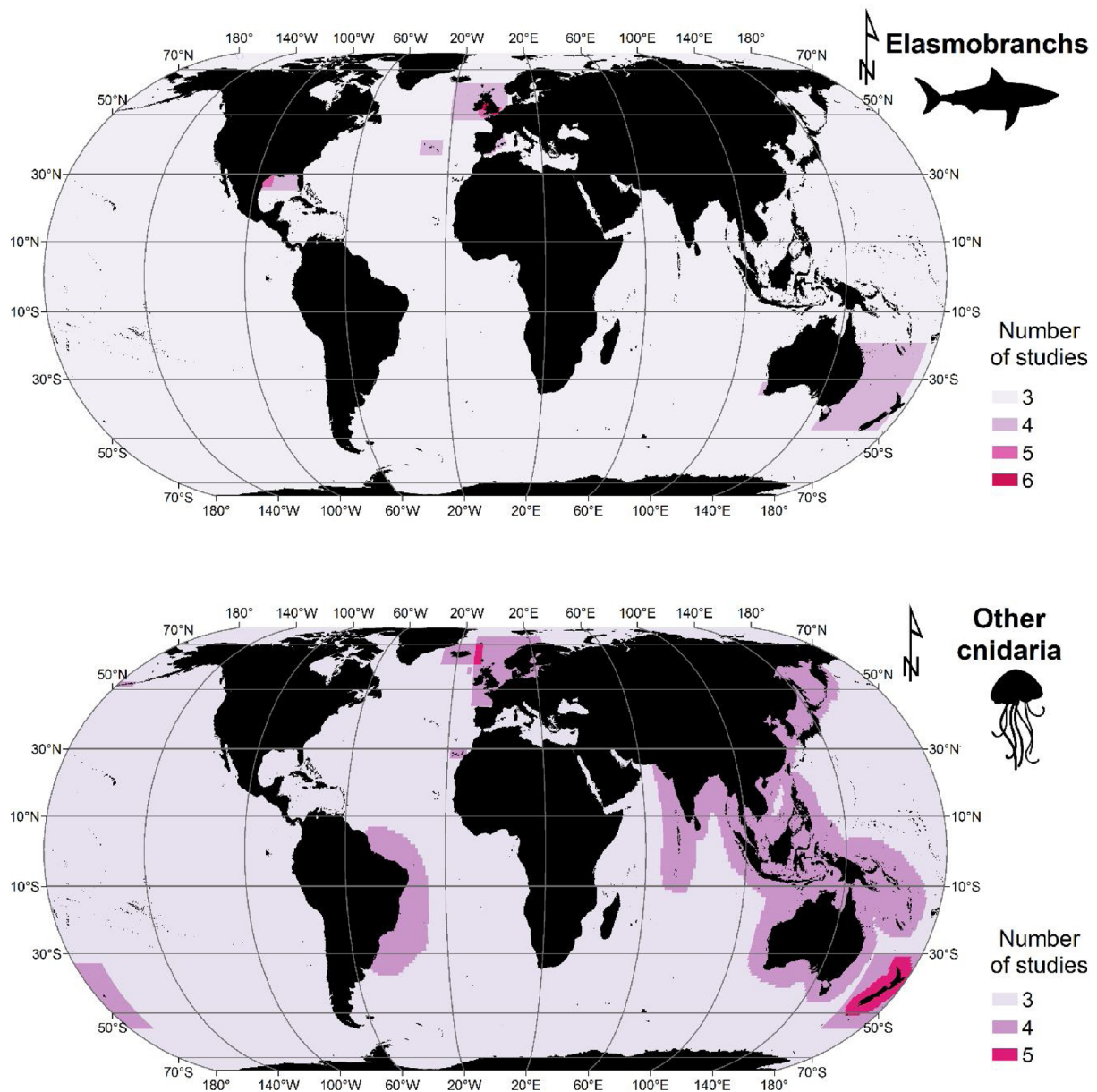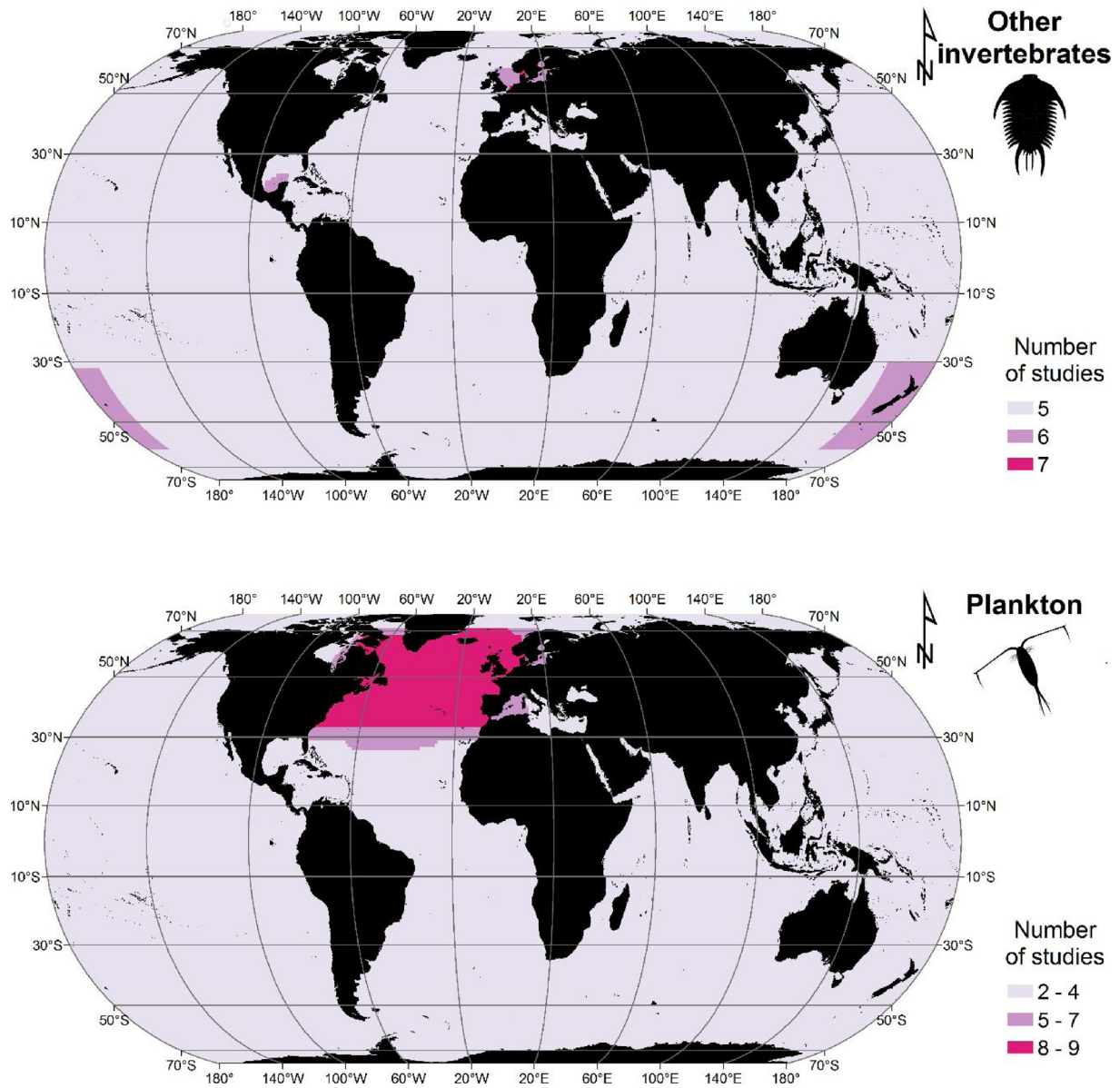
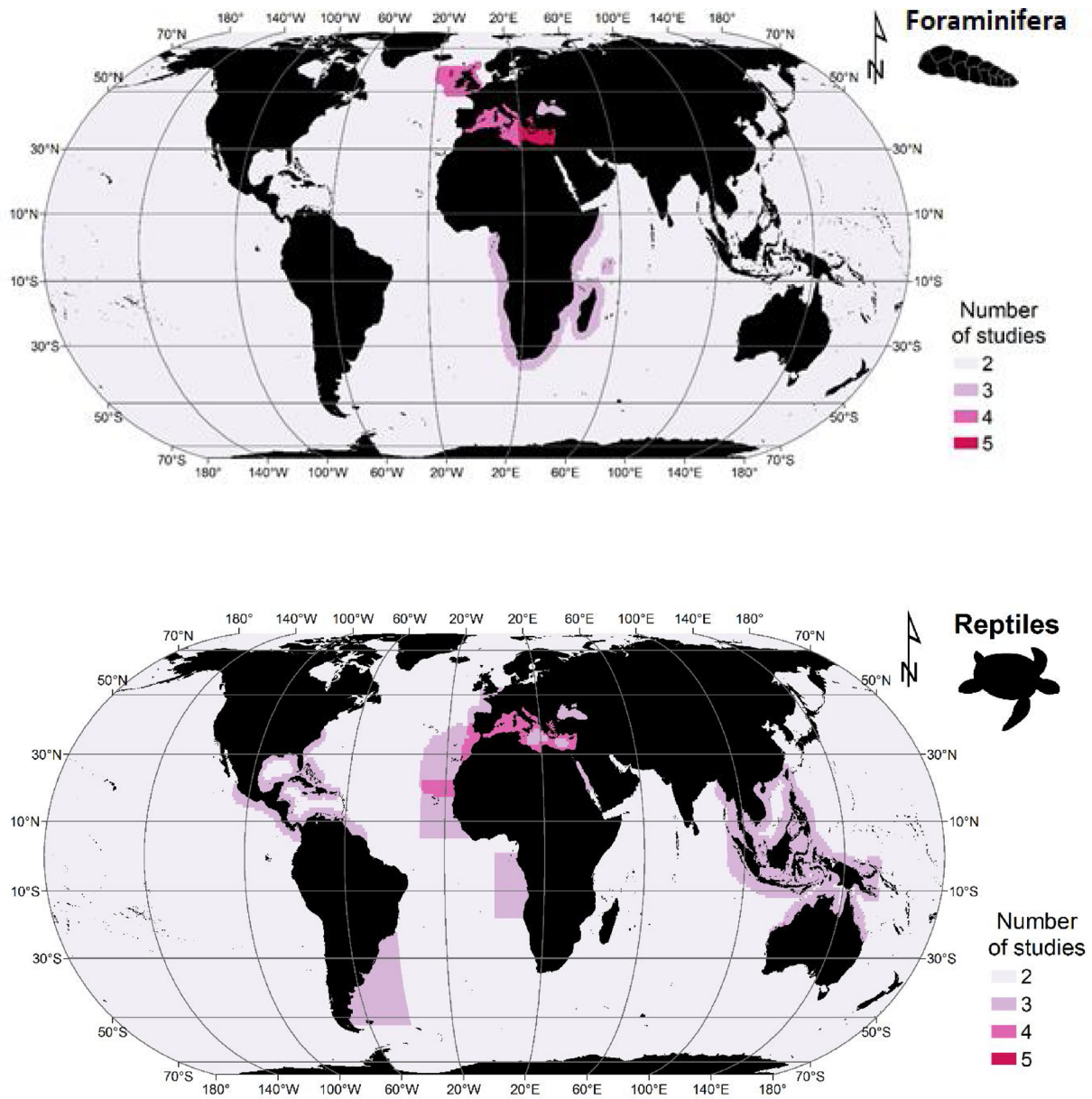**Fig. B1.** (continued)

Fig. B1. (*continued*)

Fig. B1. (*continued*)
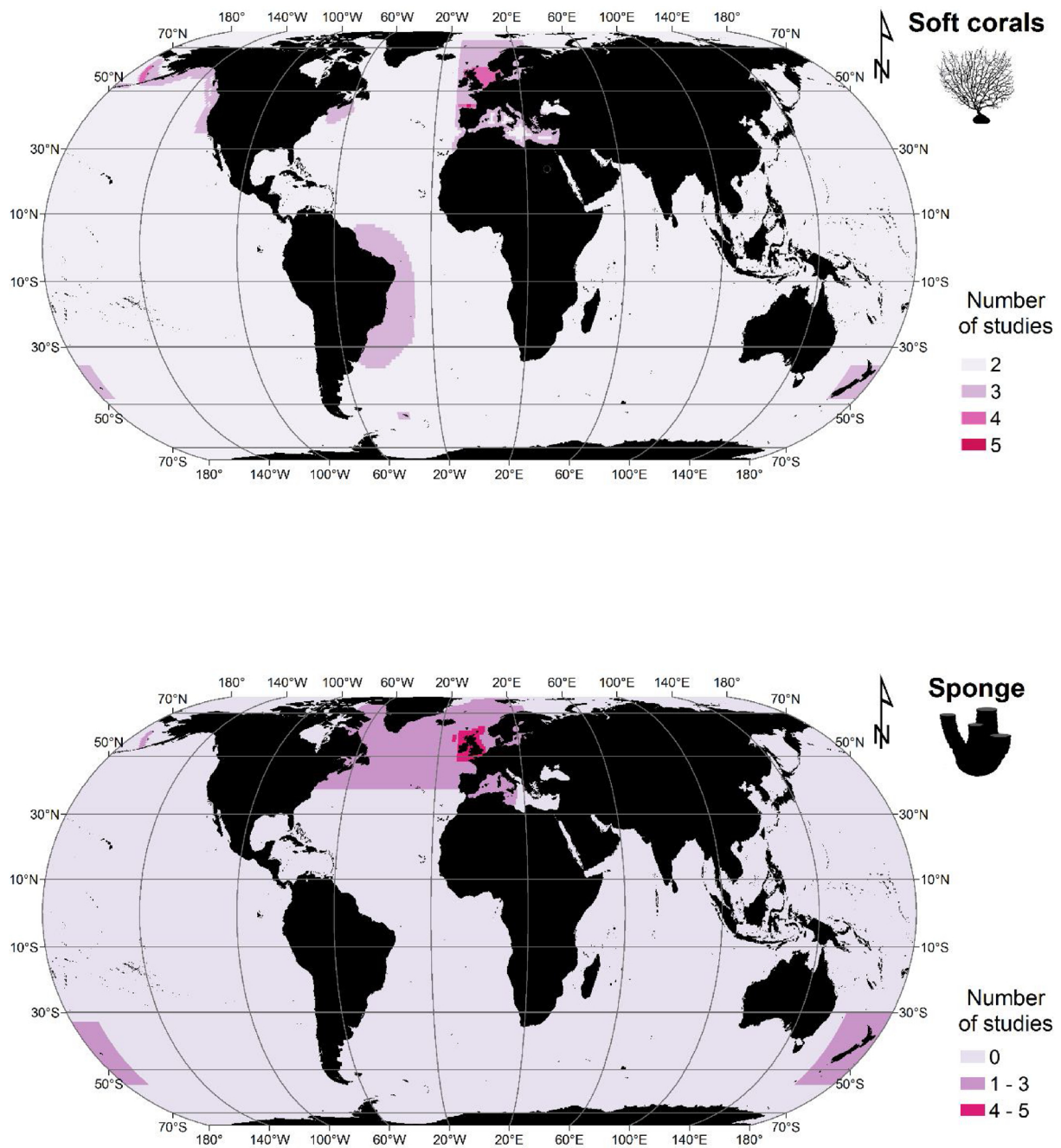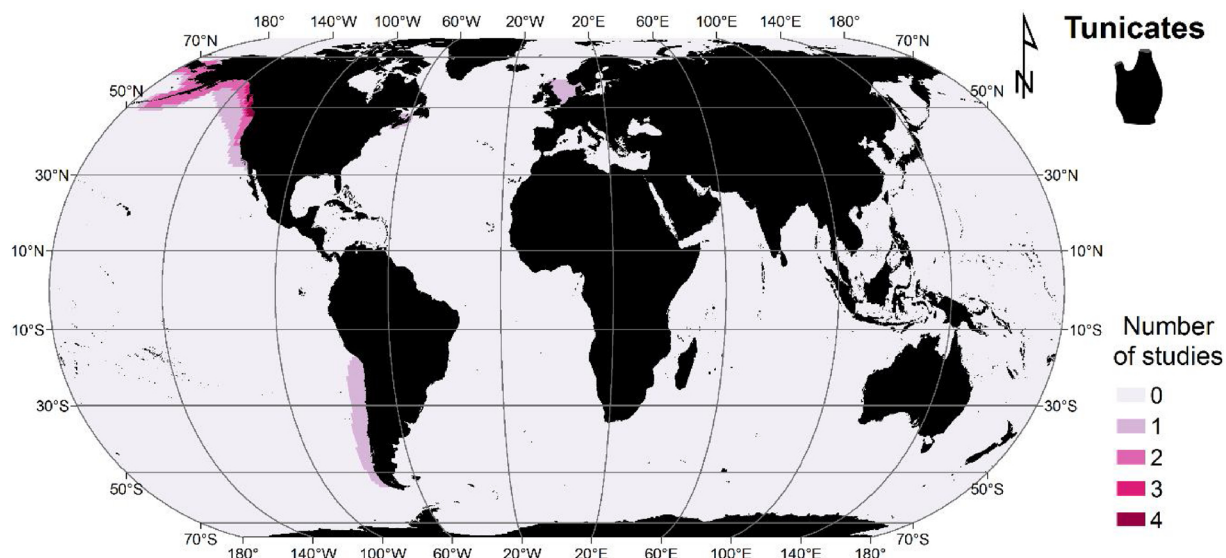
Fig. B1. (*continued*)

Fig. B1. (*continued*)

Appendix C

Table C1

List of predictor variables used to model marine species in the literature reviewed. Variables were assigned to different categories; we show how many times appeared in the articles.

CATEGORY	VARIABLE	FREQUENCY OF USE
ATMOSPHERIC VARIABLES		
	Air temperature	15
	Precipitation	9
	Wind speed	9
	Cloud cover	7
	Thermal fronts	4
	Air humidity	3
	Cyclone activity	2
	Front probability	2
	Precipitation as snow	1
ENVIRONMENTAL DESCRIPTOR VARIABLES		
	Sediment type	30
	Substrate/bottom type	27
	Ice cover	24
	Wave exposure	13
	Benthic zone	3
	Land cover	1
	Presence/absence of tidewater glacier	1
	Treatment plant effluent exposure	1
	Land cover	1
	Percentage of area with seabank	1
	Presence of land	1
	Water run-off	1
	NAO (North Atlantic Oscillation)	1
	Shore-zone type	1
	Pacific Decadal Oscillation index	1
ECOLOGICAL VARIABLES		
	Habitat type	11
	Presence/absence/biomass of other species	7
	Phytoplankton concentration	3
	Zooplankton concentration	3
	Food availability	3
	Abundance	1
	Predation pressure	1

(*continued on next page*)

Table C1 (*continued*)

CATEGORY	VARIABLE	FREQUENCY OF USE
	Biogeographic province	1
	Vegetation productivity	1
PHYSICAL VARIABLES		
	Water temperature	240
	Photosynthetically active radiation	26
	Diffuse attenuation coefficient	20
	Turbidity	8
	Euphotic depth	6
	Vertical velocity	5
	Bed shear stress	4
	Light availability	4
	Eddy kinetic energy	4
	Irradiance	3
	Solar radiation	3
	Secchi depth	3
	Wave kinetic energy	2
	Insolation	2
	Visibility	2
	Ocean advection	1
	Magnetic anomalies	1
	Cumulative thermal stress	1
	Potential energy deficit	1
	Total kinetic energy	1
	Hue-saturation intensity	1
	Potential energy anomaly	1
	Geostrophic velocity	1
	Vorticity	1
	Potential energy deficit	1
GEOGRAPHIC VARIABLES		
	Distance to shore	54
	Geographic coordinates	20
	Distance to reefs	5
	Distance to bathymetric contours	5
	Distance to seamounts	4
	Distance from colony (birds)	3
	Distance to shelfbreak front	3
	Distance to ports	3
	Distance to soft substrate	3
	Distance to freshwater streams	3
	Distance to the nearest estuary	2
	Distance to roads	2
	Distance to the nearest city	2
	Distance to rocks	2
	Distance to rocky substrate	2
	Distance to ice	2
	Distance to persistent frontal activity	1
	Distance to moraine	1
	Distance to glaciers	1
	Distance from canyons	1
	Distance to southern boundary of Antarctic circumpolar current	1
	Distance from merchant shipping routes	1
	Distance to oceanographic fronts	1
	Distance from navy exercise areas	1
	Distance from industrial areas	1
	Distance from fishing areas	1
	Distance to nearest petroleum platform	1
	Distance to river mouths	1
	Distance from sediments	1
	Distance to colored substrate	1
	Distance to tidal inlet	1
	Distance to watersheds	1
HYDRODYNAMIC VARIABLES		
	Current velocity	45
	Mixed layer depth	15
	Sea level anomalies	10
	Sea surface height	8
	Wave height	7
	Thermocline depth	5
	Tide amplitude	4
	Tidal currents	3
	Vertical flow	2
	Sea ice thickness	2
	Tides	2
	Water mass	2

Table C1 (*continued*)

CATEGORY	VARIABLE	FREQUENCY OF USE
	Beaufort sea state	1
	Wave direction	1
	Tidal state	1
	Ekman upwelling	1
	Thermocline strength	1
	Thermocline thickness	1
	Hydroperiod	1
	Current magnitude	1
	Prevalence of circumpolar deep water	1
	Pycnocline depth	1
	Coastal upwelling	1
	Geostrophic zonal currents	1
CHEMICAL VARIABLES		
	Salinity	147
	Chlorophyll-*a*	97
	Nitrate	41
	Phosphate	36
	Dissolved oxygen	36
	Primary productivity	34
	Silicate	26
	pH	24
	Calcite concentration	22
	Aragonite	13
	Saturated oxygen	12
	Alkalinity	11
	Apparent oxygen utilization	11
	Dissolved inorganic carbon	9
	Particulate organic carbon	9
	Suspended particulate matter	4
	Carbonate ion concentration	3
	Total nitrogen	2
	Ammonium	1
	Coloured dissolved organic matter	1
	Iron concentration	1
	Nitrogen oxide concentration	1
	Fluorescence activity	1
	Total phosphorus	1
	Dissolved organic matter	1
	Nutrient input	1
	Nitrogen concentration	1
TOPOGRAPHIC VARIABLES		
	Bathymetry	210
	Slope	109
	Rugosity	39
	Slope aspect	35
	Bathymetric position index	20
	Slope curvature	19
	Planimetric curvature	7
	Structure and complexity	5
	Profile curvature	5
	Topography	4
	Altitude	1
	Elevation	1
	Geomorphology	1
	Bathymetric gradient	1
	Hypsometric index	1
	Beach morphology	1
	Land use	1
TEMPORAL VARIABLES		
	Season of the year	7
	Year (calendar year)	4
	Length of day	3
	Time of the day	2
OTHER VARIABLES		
	Dust level	2
	Human population density	1
	Density of petroleum platforms	1
	Presence/absence of boat marinas	1
	Fishing effort	1
	Presence of fishing vessels	1
	Sampling depth	1
	Cargo traffic	1
	Boat speed	1
	Engine on/off	1
	Marine protected areas zoning	1

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