Universidade de Évora - Instituto de Investigação e Formação Avançada

Programa de Doutoramento em Biologia

Tese de Doutoramento

Global patterns of marine biodiversity and the potential impact of climate change

Joana Sousa e Silva Boavida-Portugal

Orientador(es) |	François Guilhaumon
	Miguel Bastos Araújo
	Rui Afonso Bairrão da Rosa

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Évora 2020

Nothing is permanent. *Everything is subject to change*.

Buddha

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LIST OF ABBREVIATIONS AND UNITS

atm	Atmosphere(s)
Chl	Clorophyll
CO_2	Carbon Dioxide
DRS	Delta Richness
EEZs	Economic Exclusive Zones
e.g.	For Example
ENM	Ecological Niche Model
ENSO	El Niño and The Southern Oscillation
ESM	Earth System Models
etc.	Et cetera
g	Gram(s)
GCM	General Circulation Model
GDP	Gross Domestic Product
GES	Gas Emission Scenario
H	Hydrogen
HS	Habitat Suitability
ISSCAAP	International Standard Statistical Classification of Aquatic Animals and Plants
IPCC	Intergovernmental Panel on Climate Change
i.e.	That is
Km	Kilometer(s)
Kg	Kilogram(s)
M	meter(s)
MCP	Maximum Catch Potential
MOC	Meridional Overturning Circulation
MRP	Maximum Revenue Potential
NOAA	National Oceanic and Atmospheric Administration
OECD	Organization for Economic Cooperation and Development
O_2	Oxygen
ppm	Parts per Million
psu	Practical Salinity Unit
p-value	Probability of the test statistic
RCP	Representative Concentration Pathway
SDM	Species Distribution Models
SPACC	Small Pelagic and Climate Change Program
SRES	Special Report on Emissions Scenarios
SSS	Sea Surface Salinity
SST	Sea surface temperature
TSS	True Skill Statistic
Ton	Tons
USD	United State Dollar (s)
µmol	Micromole(s)
%	Percentage
°C	Degree Celsius
±	Approximately

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ABSTRACT

Global patterns of marine biodiversity and the potential impact of climate change

Marine species are highly susceptible to climate change as demonstrated by several studies. However, most of these studies focus on few species or on restricted geographical areas. Within this context, the main goal of my dissertation is to characterize global patterns and forecast the effects of climate change on marine biodiversity. This work is the first macroecological approach to investigate the effects of climate change in the marine realm on key commercial marine groups, namely coastal lobsters (125 species), cephalopods (161 species) and small pelagic fish (103 species). Here I aimed to improve our understanding of how projected changes in species distribution might affect key marine species diversity, body size, assemblage composition, variations in catch, and finally infer on the potential impacts for fisheries worldwide. Using Ecological Niche Models (ENMs) the projected global diversity patterns of the analyzed species generally showed higher values in tropical areas and lower values in higher latitudes. Nonetheless, these patterns were projected to change significantly by the end of the century, with a general tendency of species tracking adequate habitat suitability to higher latitudes. The results obtained provide critical information to anticipate negative impacts of climate change on marine biodiversity and should be considered in future studies, as they highlight climate hot-spot areas or with highly vulnerable species. Ultimately, it is crucial to evaluate species adaptation potential and develop hybrid models that better can guide future political decisions on conservation and management measures.

Keywords: Climate change; marine biodiversity; ecological niche modelling; macroecology; cephalopods; lobsters; small pelagic fishes.

RESUMO

Padrões globais da biodiversidade marinha e o potencial impacto das alterações climáticas

As espécies marinhas são altamente suscetíveis às alterações climáticas, como demonstrado em numerosos estudos. Porém muitos desses estudos focam-se num número reduzido de espécies ou numa determinada área geográfica (local ou regional). Neste contexto, a presente dissertação tem como objetivo investigar os padrões globais de biodiversidade marinha e projetar como estes poderão estar modificados no final do século. Este trabalho constitui a primeira abordagem macroecológica que investiga, numa escala global, os impactos das alterações climáticas em taxa marinhos com alto interesse económico, como lagostas (125 espécies), cefalópodes (161 espécies) e pequenos peixes pelágicos (103 espécies). Os padrões globais de biodiversidade marinha para todos os taxa analisados mostram maior riqueza na zona dos trópicos e menor número de espécies nas maiores latitudes. No entanto, estes padrões podem sofrer modificações significativas até ao final do século verificando-se uma tendência generalizada das espécies migrarem para latitudes maiores de forma a encontrarem refúgio em áreas com boa adequação ambiental. Os modelos usados nesta tese (modelos de nicho ecológico) projetam alterações significativas na distribuição das espécies analisadas, com impactos profundos na riqueza e abundância em áreas vitais para a saúde dos oceanos e para as pescas, a longo prazo. Esta dissertação representa um contributo importante para o conhecimento dos padrões globais da biodiversidade nos oceanos futuros. Servindo os seus resultados para orientar estudos pormenorizados em áreas de risco elevado ou com espécies mais vulneráveis e informar a tomada de decisões com vista a proteção de espécies marinhas com elevado valor económico e ambiental. Contudo, atendendo aos efeitos das alterações climáticas já sentidos nos oceanos, é crucial avaliar a capacidade de adaptação destas espécies e encontrar modelos híbridos que melhor nos permitam orientar medidas de gestão e conservação futuras.

Palavras-chave: Alterações climáticas; biodiversidade marinha; modelos de nicho ecológico; macroecologia; cefalópodes; lagostas; pequenos peixes pelágicos.

CHAPTER 1

1. GENERAL INTRODUCTION

1. GENERAL INTRODUCTION

1.1 Global changes

In the past the main drivers of global change were solar variation, plate tectonics, volcanism, proliferation and abatement of life, meteorite impact, resource depletion, changes in Earth's orbit around the sun and changes in the tilt of Earth on its axis (UNEP, 1993). Presently, there is overwhelming evidence that the main drivers of global change are associated with the human population growth and consumption, energy use, land use changes, and pollution (Vitousek, 1994). Global emissions and the accumulation of carbon dioxide (CO_2) in the atmosphere rose dramatically during the 20th century (Fig. 1A). Since the industrial revolution fossil fuel combustion and industrial processes have released tons of carbon into the atmosphere and, at present, the value surpasses six billion metric tons per year (IPCC, 2013). Consequently, atmospheric CO_2 concentrations have greatly increased from 280 ppm at pre-industrial levels to more than 400 ppm nowadays (NOAA, 2018).

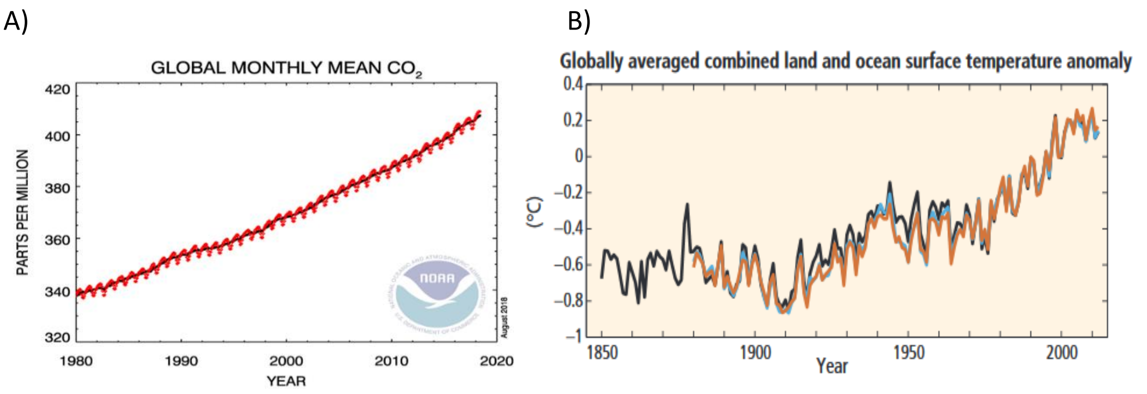

Fig. 1 A) Carbon dioxide concentration levels from previous 800 thousands of years until August 2018 [Source: NOAA (2018)]; B) projected surface temperature changes for the late 21st century - temperatures are relative to the period 1850-2012; colors indicate different data sets [Source: IPCC (2014)].

Climate experts predict that future levels may reach 1000 ppm by the end of the century (IPCC, 2014) if anthropogenic emissions remain within the same rates. Carbon accumulation overloads the atmosphere, and the consequently trapped heat causes Earth to warm. The globally averaged combined land and ocean surface temperature data show a linear warming trend of 0.85°C [0.65 to 1.06] over the period 1880 to 2012 (Fig. 1B). The increasing CO_2 concentrations in the atmosphere can remain in the atmosphere or can be absorbed by the terrestrial biosphere or by the oceans (Le Quéré *et al.*, 2009).

1.1.1 Oceans

The global ocean regulates our climate and drives the weather, determining rainfall, droughts and floods. It also play a key role in mitigating climatic changes, sequestering heat and carbon from the atmosphere. The transport of heat, freshwater and dissolved gases by oceanic currents can have an important effect on regional climates, and the large-scale Meridional Overturning Circulation – MOC -, also referred to as thermohaline circulation (Fig. 2), is known to influence the climate on a global scale (Vellinga & Wood, 2002). Large-scale impacts of climate change on oceans are expected to include increases in sea surface temperature and mean global sea level, decreases in sea-ice cover, and changes in salinity, wave conditions, dissolved gases and overall ocean circulation (Brierley & Kingsford, 2009).

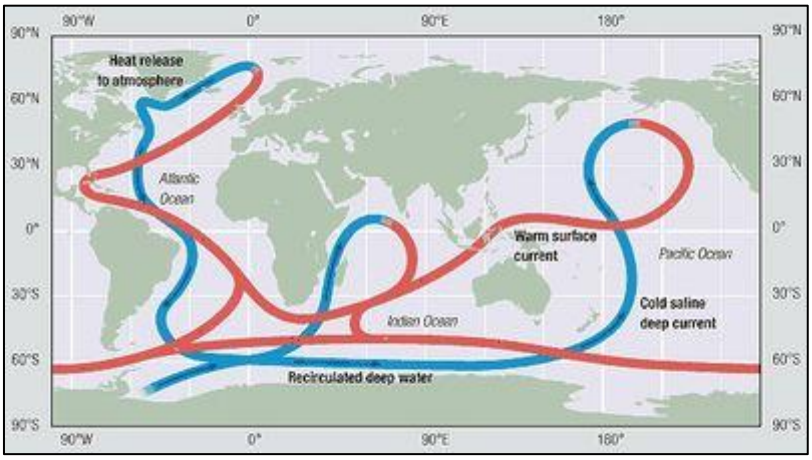

Fig.2 Meridional Overturning Circulation [Source: IPCC (2007)].

Changing climatic conditions and the increased freshwater influx in the polar regions have caused sea ice retreats from the coastline of Arctic countries from 150 km to 200 km (Stendel *et al.*, 2008). The loss of ice in the Polar Regions could lead to a sudden acceleration of global warming, as ice reflects radiation and heat from the sun back into space. The absence of sea ice combined with ocean warming will lead to more evaporation and rainfall occurring in these sensitive regions, which in turn will speed up sea ice loss. Global analyses show long-term freshening in the subpolar latitudes and a salinification of shallower parts of the tropical and subtropical oceans, which is projected to intensify under climate change scenarios (Palmer *et al.*, 2019- Fig.3 SSS). This could lead to significant changes in the atmospheric hydrological cycle over the oceans and in changes in global oceanic circulation.

Furthermore, changes in the storage of heat and in the distribution of ocean salinity cause the ocean to expand or contract and hence change the sea level both regionally and globally. Global mean sea level rise is projected to continue during the 21st century, at a faster rate than observed from 1971 to 2010. Earth System Models (ESM) project a global rise in sea level for all RCP scenarios by the end of the 21st century, ranging from 0.26 to 0.82 m (IPCC, 2014). By the end of the 21st century, it is projected that sea level will rise in more than about 95% of the ocean area, with about 70% of the coastlines worldwide projected to experience a sea level change within ±20% of the global mean (Mimura, 2013).

Over the last 200 years, the ocean has absorbed around a third of the CO_2 produced by human activities and has absorbed over 90% of the extra heat trapped by the rising concentrations of atmospheric greenhouse gases (Gattuso *et al.*, 2015). As a consequence of heat absorption from the atmosphere, oceans are becoming warmer, at a rate of approximately 0.1°C per decade, over the last decades. It is predicted that global mean surface temperature will increase between 1.1-6.4°C by the end of the century (Fig. 3 – SST), depending on the scenario used (IPCC, 2014).

By absorbing CO_2, the ocean are also becoming more acidic – at a faster rate than any other period in the past 65 million years. Since pre-industrial times, ocean's pH has already dropped an average of 0.1 units (Dupont & Pörtner, 2013), and it is predicted that this process will lead to an increase of 15% to 109% in ocean acidity (Fig. 3 – pH), according to the scenario, by end century (IPCC, 2014).

The same physical processes that affect CO_2 affect dissolved oxygen (O_2) in the ocean, but O_2 is not affected by changes in atmospheric concentration (Hinkle, 1994). Changes in oceanic O_2 concentration occur due to the changes in the physical or biological processes within the ocean, such as rate of renewal of thermocline waters, water formation, upwelling or biological export and respiration.

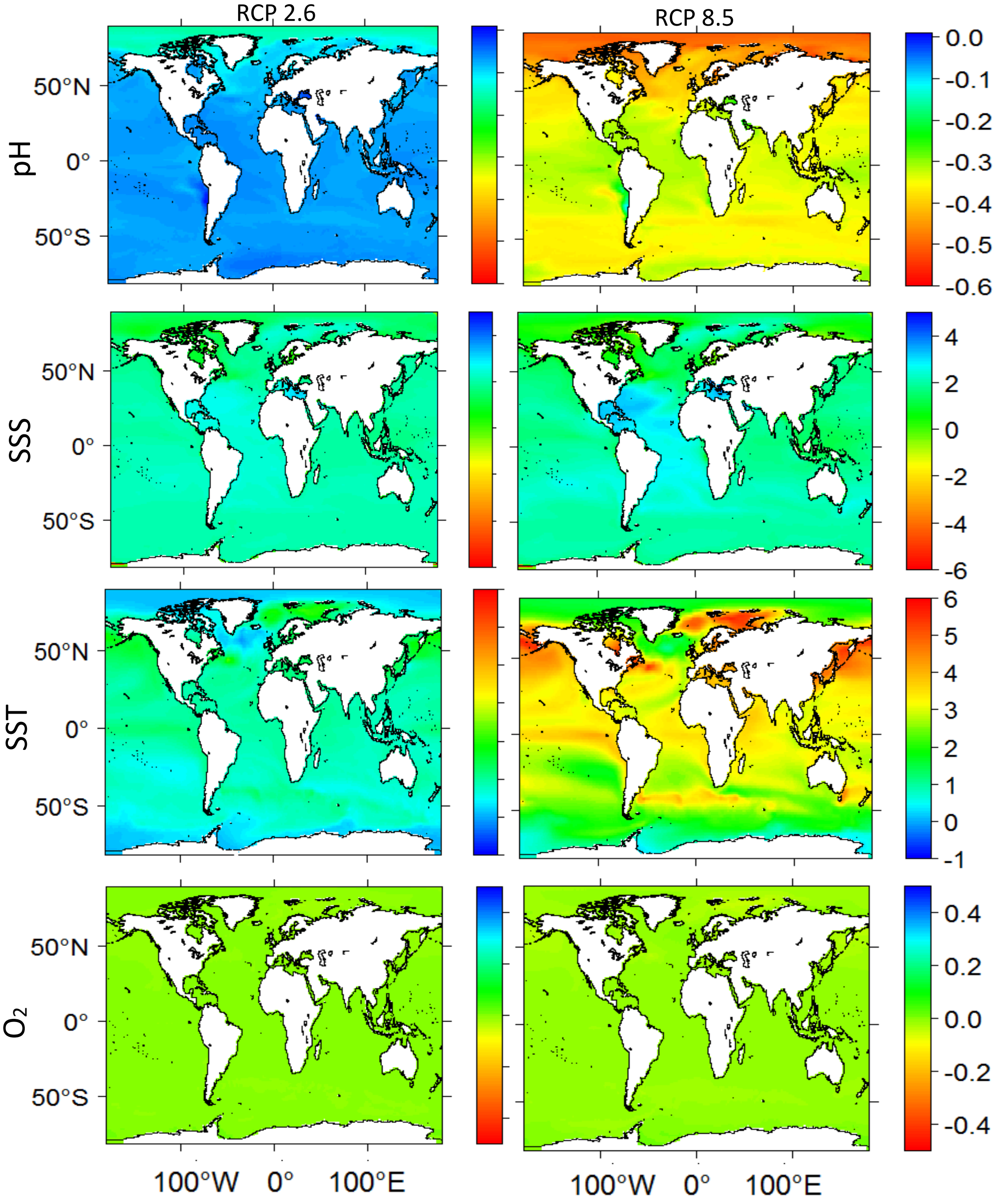

Fig.3 Predicted changes between the baseline and the end-century period, according to IPCC most extreme scenarios (RCP 2.6 and 8.5) for the climatic variables used in this thesis: pH at surface ('pH', in mol H kg^{-1}), sea surface salinity ('SSS'), sea surface temperature ('SST', in °C), dissolved oxygen concentration at surface ('O_2', in mol m^{-3}).

Dissolved oxygen changes in the ocean thermocline has generally decreased since 1960, at a mean rate of 0.63 µmol kg^{-1} per decade (Stramma *et al.*, 2012). This long-term deoxygenation trend is consistent with the expectation that warmer waters can hold less dissolved oxygen (solubility effect), and that warming-induced stratification leads to a decrease in the transport of dissolved oxygen from surface to subsurface waters (stratification effect; for review see Breitburg *et al.*, 2018 ; Fig. 3 - O2).

Future ocean climate-related changes are expected to make organisms more susceptible to the impact of other pressures, such as overfishing, habitat destruction, and pollution. Climate change will challenge the marine biota across multiple levels of biological organization, from molecular to organismic level, and are predicted to elicit cascading effects on population, community and ecosystems dynamics (e.g. Beaugrand *et al.*, 2015). When species persistence is affected by climate change-related conditions, organisms can respond by acclimatizing and adapting to new conditions, or by shifting their geographical distribution (Pecl *et al.*, 2017). Changes in biodiversity may alter the community structure and possibly disrupt ecological interactions, enhancing the risk of species and ecosystems extinction (Camill, 2010).

1.2 Impacts of climate change on marine biota and ecosystems

For centuries, people have regarded the ocean as an inexhaustible source of food and a convenient dumping ground, often regarded too vast to be affected by anything we do. But in just a few decades, it became clear that the ocean has limits and that in many important parts of our seas the sustainability thresholds have been breached. The intensity of climate-related impacts varies with the interaction between climate-related hazards, with the vulnerability of the natural systems, with their ability to adapt and with the exposure to human impacts. Rising rates and magnitudes of warming and other changes in the climate system, accompanied by ocean acidification, increase the risk of severe, in some cases irreversible, detrimental impacts. Some risks are particularly relevant locally, while others are global (Fig. 4). The overall risks of future climate change impacts can be reduced by limiting the rate and magnitude of climate change, but the precise levels of climate change sufficient to trigger abrupt and irreversible change remain uncertain (IPCC, 2014).

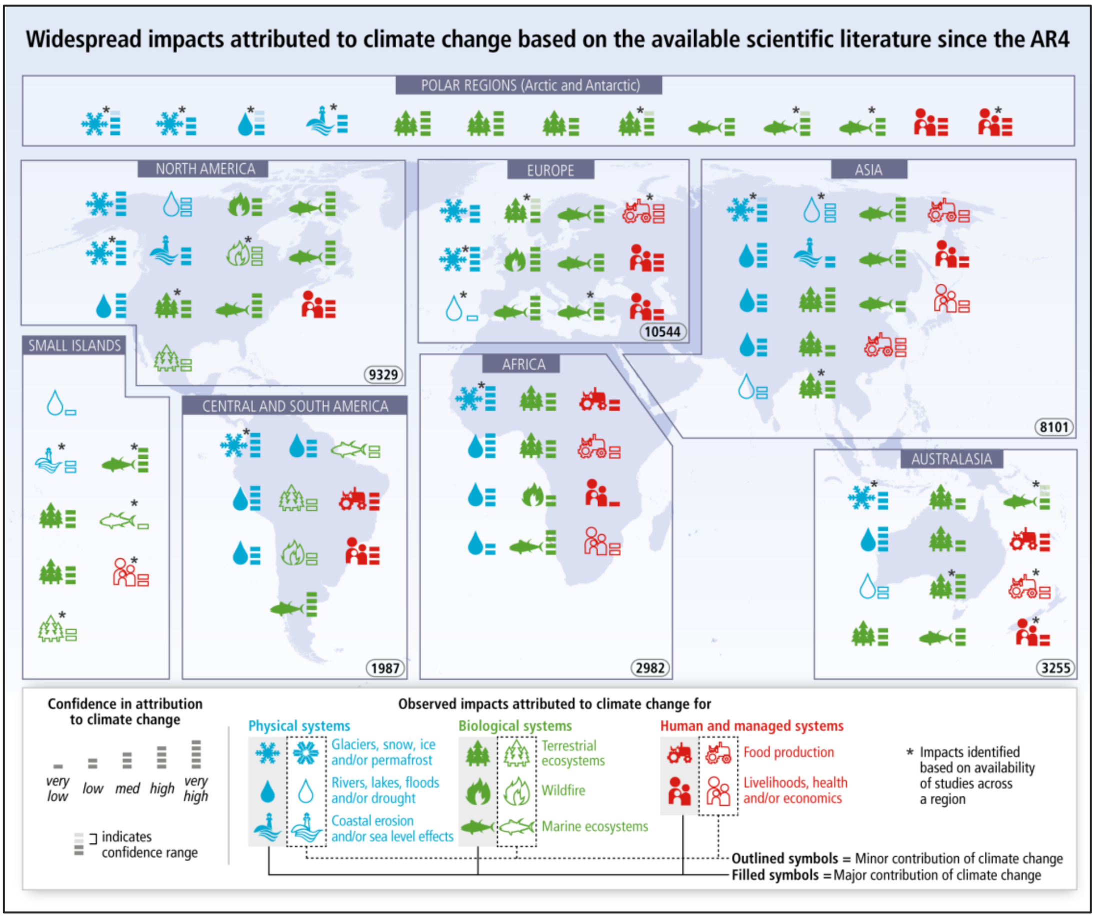

Fig. 4 Global impacts attributed to climate change based on the available scientific literature since the IPCC Fourth Assessment Report (AR4 in 2007). Symbols indicate categories of attributed impacts, the relative contribution of climate change (major or minor) to the observed impact and confidence in attribution [Source: IPCC (2014)].

For example, ocean acidification reduces the ability of coral reefs to re-establish from disturbances such as bleaching, cyclones and crown-of-thorns starfish outbreaks. If current rates of temperature rise continue, the ocean will become too warm for coral reefs by 2050 (Hoegh-Guldberg *et al.*, 2017). This would potentially mean a major disruption to at least 25 percent of the biodiversity in the ocean, as well as the loss of productive fisheries and significant impacts on industries such as tourism. The loss of reefs as a barrier would increase the exposure of coastal areas to waves and storm systems.

Coastal systems and low-lying areas are also increasingly experiencing adverse impacts from sea level rise – submergence, coastal flooding, and coastal erosion. The loss of coastal ecosystems such as mangroves and seagrass beds increases vulnerability of coastlines and people to the impacts of climate change. Many low-lying developing countries and small island states are expected to face severe impacts that, in many cases, could result in displacement of people, damage to ecosystems, and adaptation costs amounting to several percentage points of Gross Domestic Product (GDP) (UN-OHRLLS, 2015).

The best recorded climate-change-induced ecological consequences are changes in *phenology*, i.e., in timing of vegetation development (Menzel & Fabian, 1999), in spawning date in frogs and toads (Beebee, 1995), return date of migrant birds (Hüppop & Hüppop, 2003) and butterflies (Sparks *et al.*, 2005), egg hatching date in insects (Visser & Holleman, 2001), laying dates in birds (Crick *et al.*, 1997), etc. And in *range shifts*, in the distribution of butterflies (Parmesan, 1999), breeding range (Thomas & Lennon, 1999) or overwintering range (Austin & Rehfisch, 2005) of birds and in distributions of marine biodiversity (Cheung *et al.*, 2009; Poloczanska *et al.*, 2013), etc. Less widespread documented consequences of climate change are shifts in body size (Millien *et al.*, 2006; Barange *et al.*, 2010) and in changes in the strength of competition between species (*e.g.* Jiang & Morin, 2004).

There are several studies exploring latitudinal *range shifts* on marine species, as a response to environmental change (e.g. Perry *et al.*, 2005; Mueter & Litzow, 2008; Jones & Cheung, 2014; Sunday *et al.*, 2015) and/or depth range shifts (Dulvy *et al.*, 2008). Such species responses may lead to local extinction and invasions, resulting in changes in the pattern of marine species distributions and richness. Local extinction refers to a species ceasing to exist in an area although it still exists elsewhere, while invasion refers to the expansion of a species into an area not previously occupied by it. Overall, changes in pattern of species richness may disrupt marine biodiversity and ecosystems, and impact commercial fisheries (e.g. Roessig *et al.*, 2004; Ainsworth *et al.*, 2011; Cheung *et al.*, 2013b; Lam *et al.*, 2016). A review (Poloczanska *et al.*, 2013) of recent literature on quantitative analysis of the effect of anthropogenic climate change on community assemblages or distributional range of marine fish and invertebrates shows that the majority of the reviewed papers focus on a regional scale or on limited taxa. The lack of large-scale studies that encompasses a wide array of marine species is in contrast to the situation prevailing in the terrestrial realm. The climate change-related impacts on marine biodiversity are projected to be intensified in the future, differing geographically and among taxonomic groups (*e.g.* Harley *et al.*, 2006; Mellin *et al.*, 2012; Caputi *et al.*, 2013; Fernandes *et al.*, 2017; FAO, 2018). Global perspectives on the impact of climate change on a wide range of marine species are vital to obtain a more complete picture of the climate change problem.

1.3 Fisheries in a changing ocean

One of the most direct impacts of climate change on marine ecosystem services is through fisheries. Given the significant increase in human population and demand for secure, sufficient and safe food supplies, it is critical to predict and anticipate the nature and magnitude of potential impacts of climate change on food production. Global marine fish landings are estimated officially at 80-85 million ton, with corresponding mean annual gross revenues around USD 100 billion annually (Swartz *et al.*, 2012). Accounting for unreported catches, a recent study (Pauly & Zeller, 2016) updated the likely "true" annual global catch to be about 130 million ton. The global fisheries sector supports the livelihoods of between 660 to 820 million people worldwide, directly or indirectly, which is about 10–12% of the world's population (FAO, 2016). Fish also provides more than 2.9 billion people with 20% of their animal protein needs and is a crucial source of micronutrients (Golden, 2016).

The consequences of fisheries collapse are complex. The ocean's once abundant fisheries are increasingly unable to feed and provide livelihoods for the world's rapidly expanding population. Average fish consumption per capita have been globally increasing from 9.9kg in the 1960s to 19.2kg in 2016 (FAO, 2016). Poor coastal communities who rely most directly on the ocean for food and livelihoods are particularly vulnerable – and often unfairly disadvantaged. Their vulnerability is a result of both their geographical location as well as their poverty situation. Being located at the waterfront, fishing and fish farming communities are exposed to climate related extreme events and natural hazards, such as hurricanes, cyclones, sea level rise, ocean acidification, floods and coastal erosion (Kalikoski *et al.*, 2018). Hence, climate change impacts could fundamentally alter the fishing industry in these communities (WWF, 2015).

Changes in ocean conditions are projected to beget shifts in the distribution range of marine species (e.g. Lam *et al.*, 2016; Fernandes *et al.*, 2017; Cheung *et al.*, 2018; Lotze *et al.*, 2019), changes in primary and secondary productivity, and shifts in timing of biological events (Pörtner, 2014). Marine species are gradually moving away from the equator into cooler waters, and, as a result, species from warmer waters are replacing those traditionally caught in many fisheries worldwide. These shifts could have negative effects including loss of traditional fisheries, decreased in profits and jobs, conflicts over new fisheries that emerge because of distribution shifts, food security concerns and a large decrease in catch in the tropics (Fig. 5; Cheung *et al.*, 2013a; Pinsky *et al.*, 2018; Free *et al.*, 2019). Sumaila and Cheung (2010) estimated that the fishing sector may, globally, suffer from a \$17–\$41 billion loss in annual landed value, depending on the climate change severity, which may result in an annual loss in household income between \$6 – \$14 billion. They also reinforce the idea that the impacts to fishing sectors in developing countries are estimated to be 2–3 times higher than those for developed countries, under all the scenarios considered in the study.

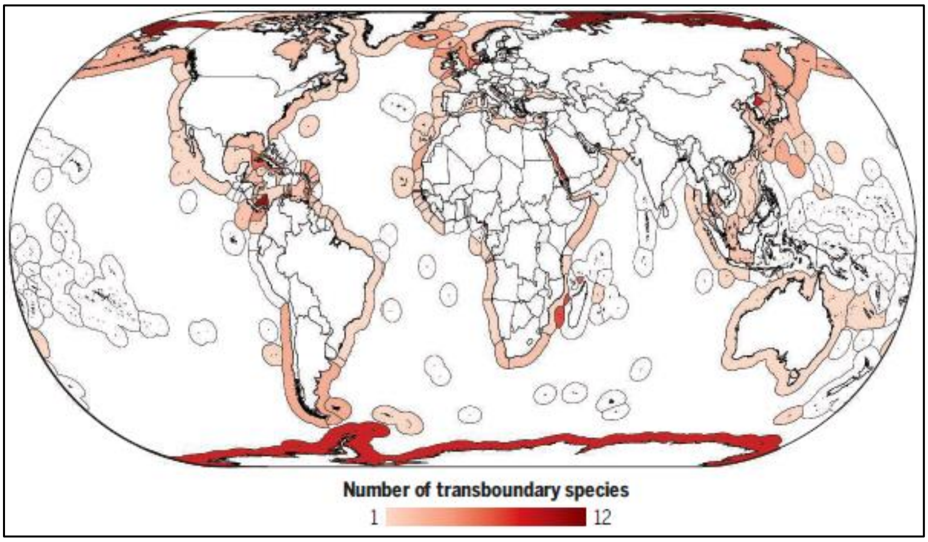

Fig. 5 Exclusive Economic Zones projected to contain one or more new fishery stocks by 2100, using RCP 8.5 scenario [Source: Pinsky et al. (2018)].

Identifying responses to climate change is complicated by species interactions and multiple stressors. Major marine habitats and biodiversity hotspots are projected to encounter cumulative impact from changes in temperature, pH, oxygen and primary production by the end of 21st century (Mora *et al.*, 2013). Acidification and hypoxia are projected to reduce maximum catch potential (MCP) in both the North Atlantic and Northeast Pacific (Ainsworth *et al.*, 2011; Cheung *et al.*, 2011). The combined effects of the projected distributional shifts and changes in ocean productivity under climate change are expected to lead to changes in species composition (Beaugrand *et al.*, 2015) hence in the global redistribution of MCP, with projected increases in MCP in high latitudinal regions and decreases in the tropics (Fig. 6). This further highlights high vulnerabilities in the economies of tropical coastal countries (Johnson & Welch, 2010).

Changes in O_2 content, as well as warming, are projected to drive a global decrease of community-averaged maximum body size (Cheung *et al.*, 2012), which may affect natural mortality rates and trophic interactions, and reduce yield-per-recruit and thus potential catch. Responses of exploited marine species and their fisheries may interact with other human stressors such as overfishing, exacerbating their impacts (e.g. Lindegren *et al.*, 2010; Ainsworth *et al.*, 2011).

Resource overexploitation appears to be the single most important factor directly threatening the sustainability of many commercial fisheries in Organization for Economic Cooperation and Development (OECD) countries (OECD, 2017). Overexploitation increases the vulnerability of fisheries to climate variability because few fish are left in the stock to grow and multiply in a year of poor recruitment. On the other hand, chronic levels of pollution are known to reduce marine and freshwater fish fecundity (Kime, 1995), decrease freshwater supply (which exacerbates low dissolved-oxygen concentrations), increase solid transport from erosion, and increase habitat fragmentation in inland waters (Carmignani & Roy, 2017). Development of marine aquaculture may also be affected by a decreasing availability of sites with cool enough surface water temperature and by increased susceptibility to disease (FAO, 2018).

Through species shifts climate change may also cause overlap of habitats of species targeted by fishing with habitat of threatened species, potentially increasing the chances of the latter being caught as bycatch (Jones *et al.*, 2013). Moreover, differences in vulnerability and adaptive capacity of species to changing environmental and ecosystem conditions will affect the response of fisheries to climate change (e.g. Griffith *et al.*, 2011; Bell *et al.*, 2013). Analyses of fish physiological response to climatic changes have shown significant detrimental, or even deleterious, effects *(e.g.* Rosa *et al.*, 2014*;* Faleiro *et al., 2016;* Pimentel *et al., 2016).* Unfortunately, current knowledge appears to be limited mostly to single key species, abstracted from the wider ecosystem context that supports fisheries production. It is likely that extrapolation from these limited biological principles will provide only a bounded foresight, but understanding of how the projected changes will influence global fisheries is vital (Santos *et al.*, 2016).

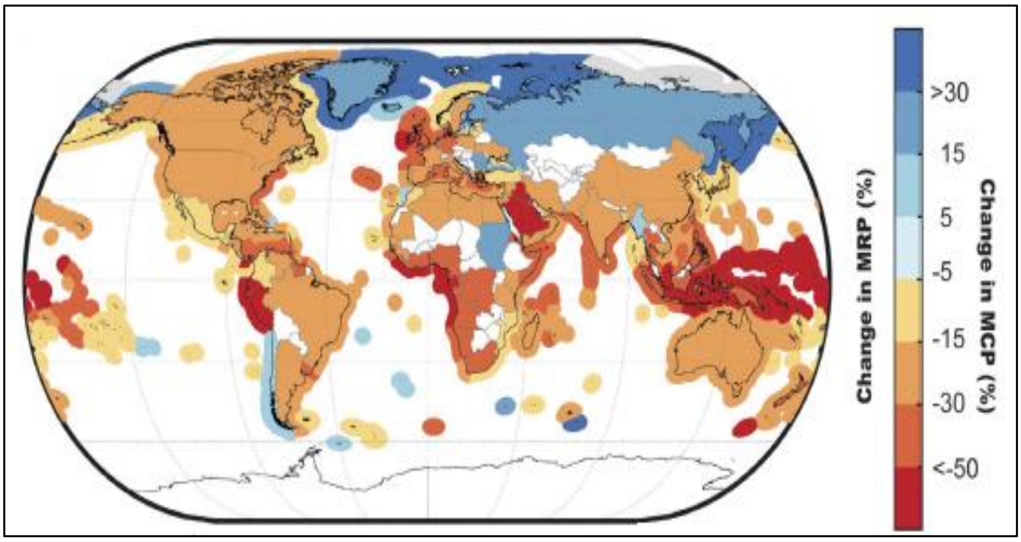

Fig. 6 Mean change in projected maximum catch potential (MCP) of 280 Exclusive Economic Zones (EEZs) and mean change in projected maximum revenue potential (MRP) of 192 fishing nations by mid-century, under RCP 8.5 scenario [Source: Lam et al. (2016)].

1.4 Ecological Niche Models

As climate change is increasingly affecting ocean physical and biogeochemical environment (Halpern et al., 2008; Crain et al., 2009; Hoegh-Guldberg & Bruno, 2010; Pörtner, 2014), several studies have explored the projected impacts in marine biodiversity (e.g. Hoegh-Guldberg *et al.*, 2008; Fisher *et al.*, 2010; Hofstede *et al.*, 2010; Hall *et al.*, 2013; Gattuso *et al.*, 2015; Frölicher *et al.*, 2018). Within this context, statistical frameworks like Ecological Niche Models [ENMs - also known as Species Distribution Models (SDMs)], have received significant attention in the terrestrial realm and have been used for over two decades to project the potential effects of climate change on species distributions (*e.g.* Peterson *et al.*, 2002; Araújo & Rahbek, 2006;

Thuiller *et al.*, 2011; Garcia *et al.*, 2014). But despite their wide range of theoretical and applied questions in the terrestrial realm, marine-based applications remain relatively limited (*e.g.* Cheung *et al.*, 2009; Lasram *et al.*, 2010; Pereira *et al.*, 2010; Kaschner *et al.*, 2011; Planque *et al.*, 2011; Robinson *et al.*, 2011; Albouy *et al.*, 2012; Jones & Cheung, 2014; Robinson *et al.*, 2017).

ENMs simulate the distribution of species in geographical space relative to climate. They are correlative models that create statistical relationships between observed presences of a species with values of environmental variables at those sites (Fig. 7). These models have several uses, but can be used under future climatic conditions to obtain an estimate of how species ranges may shift with climate change. The typical output of ENMs is a map of a species' potential range (or potential habitat), either in the present or in both the present and the future (for review in ENMs see Elith & Leathwick, 2009; Araújo & Peterson, 2012).

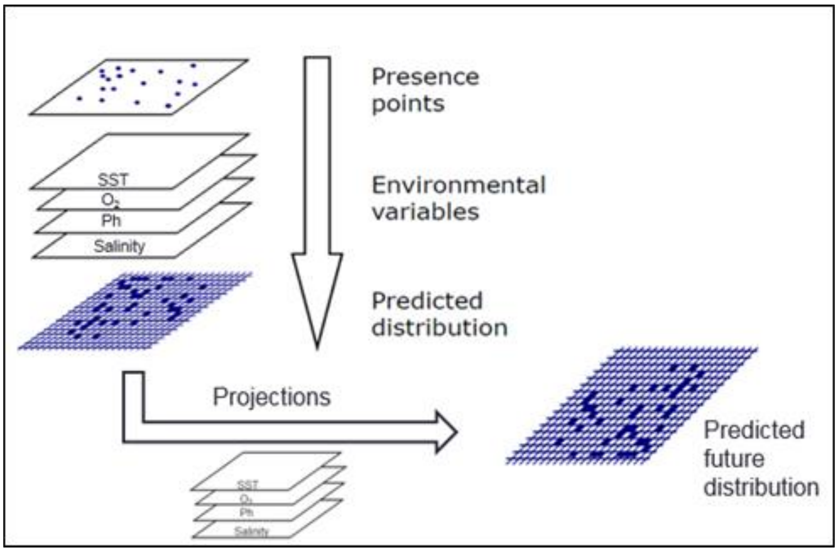

Fig. 7 Ecological niche models for climate change projections schematic.

Although the relationship between climate and species ranges is well established (Woodward & Williams, 1987), as it is based on paleoecological studies (Webb & Bartlein, 1992), using ENMs to predict the impact of global warming on species distributions requires some assumptions and has several limitations (Elith & Graham, 2009). First, ENMs assume that species distributions is in equilibrium with the climate (*i.e.* species occupy all climatically suitable areas and are absent from all unsuitable ones; Araújo & Pearson, 2005). A second assumption is stationarity of the empirical relations defined between environmental conditions and species distributions. This is reasonable when predicting for conditions that have analogues in the historical record, but becomes less reliable for responses to extreme events or for the novel conditions expected under climate change (Williams *et al.*, 2007). Third, caution is advised when interpreting ENM's results, as the relationships inferred may not adequately describe the factors determining species distributions. Spatial data on species distributions reflect the realized rather than the fundamental ecological niche (Fig. 8; Araújo & Peterson, 2012). This realized niche implicitly reflects biotic interactions as competition, mutualism, predation and barriers to species dispersal, not only environmental conditions (sampling incompleteness (either in geographical or environmental space) may also contribute to this (Peterson, 2011).

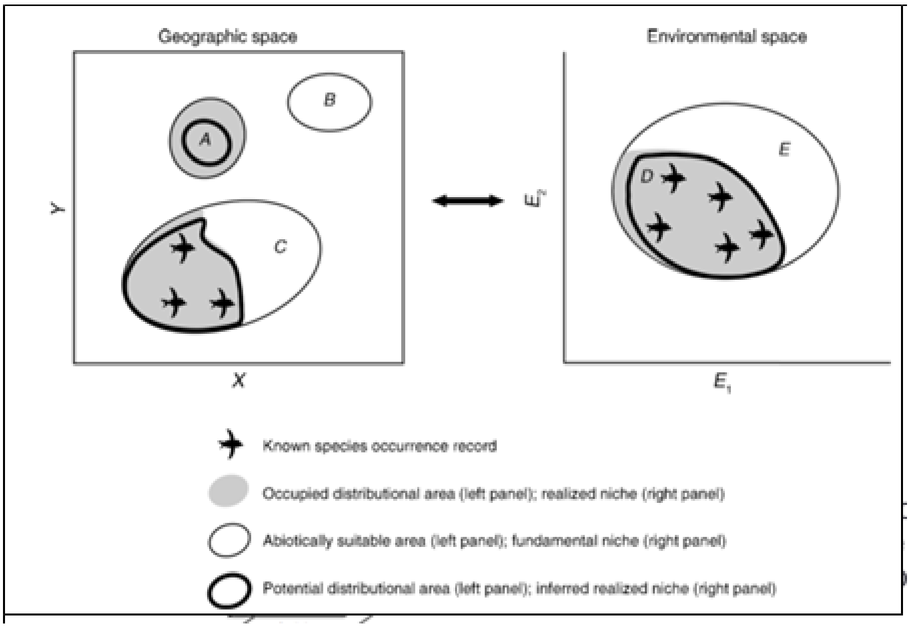

Fig. 8 Illustration of the relationship between the different distributional areas of a species in geographic and environmental space, and its modelled distribution and niche [Source: Araújo & Peterson (2012)].

Lastly, ENMs are a "static" approach to modelling a species distribution, as they typically do not take into account species ability to move on geographical space (dispersal or migration), or do so in simple ways – usually assuming "all or nothing" dispersal or migration into new suitable habitat, or limited dispersal to contiguous suitable habitat (Araújo & Guisan, 2006; Heikkinen *et al.*, 2006). Regardless of these limitations, ENMs use is widespread, with them being continually modified and improved to better cope with methodological limitations (Guisan *et al.*, 2006; Araújo & New, 2007; Nógues-Bravo, 2009; Araújo & Peterson, 2012; Fordham *et al.*, 2012; Guisan *et al.*, 2013; Garcia *et al.*, 2014; Araújo *et al.*, 2019). Offering a good solution for undertaking relatively rapid (and cheap) analysis over a large amount of species and/or geographical space.

Despite ENMs many assumptions and the uncertainty associated with their projections, particularly in a climate change context, they present valuable tools with enormous outreach. Knowing the level of uncertainty in their outputs is important not only for managers to understand and manage the risk of actions, but also for scientists to focus their efforts in advancing ecological niche modelling. Following known recommendations on uncertainty reduction can help ENMs achieve a more realistic picture of the future impacts of climate change on biodiversity (Araújo *et al.*, 2019).

1.5 Objectives and thesis outline

Given the urgent need for an understanding of the consequences of climate change on the world’s oceans, the main goal of this dissertation is to characterize global patterns and forecast the effects of climate change on marine biodiversity. Overall, I aimed to investigate the effects of projected climate changes, under different mitigation scenarios, on the distribution of key commercial marine species worldwide, namely coastal lobsters (125 species), cephalopods (161 species) and small pelagic fish (103 species) species. I also aimed at improving understanding of how the projected changes in species distribution might impact important marine species diversity, body size, assemblage composition, variations in catch, and finally infer on the potential impacts for fisheries worldwide. The thesis is composed of five chapters and includes three scientific papers, one published and two submitted in peer-reviewed international journals, which can be found from chapter 2 to 4.

Specifically, the main objectives of the chapters are presented below:

1. Give an overview on climate change in marine environment and on Ecological Niche Models (Chapter 1);
2. Predict the impacts of climate change on coastal lobster distribution and possible effects on fisheries worldwide (Chapter 2);

3. Evaluate the patterns of cephalopod coastal diversity and potential changes under climate change in richness, mean body size and assemblage composition (Chapter 3);
4. Analyse the impact of climate change in small pelagic fish species richness, catch potential and geographic range size (Chapter 4);
5. Resume the work presented in this thesis and give an outlook on future perspectives (Chapter 5).

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CHAPTER 2

1. CLIMATE CHANGE IMPACTS ON THE DISTRIBUTION OF COASTAL LOBSTERS

* Boavida-Portugal J, Rosa R, Calado R, Pinto M, Boavida-Portugal I, Araújo MB, Guilhaumon F. (2018) Climate change impacts on the distribution of coastal lobsters. Marine Biology. 165: 186. DOI: 10.1007/s00227-018-3441-9

2. CLIMATE CHANGE IMPACTS ON THE DISTRIBUTION OF COASTAL LOBSTERS

2.1 Abstract

Coastal lobsters support important fisheries all over the world, but there is evidence that climate-induced changes may jeopardize some stocks. Here we present the first global forecasts of changes in coastal lobster species distribution under climate change using an ensemble of ecological niche models (ENMs). Global changes in richness were projected for 125 coastal lobster species for the end of the century, using a stabilization scenario (4.5 RCP). We compared projected changes in diversity with lobster fisheries data and found that losses in suitable habitat for coastal lobster species were mainly projected in areas with high commercial fishing interest, with species projected to contract their climatic envelope between 40 and 100%. Higher losses of spiny lobsters are projected in the coasts of wider Caribbean/Brazil, eastern Africa and Indo-Pacific region, areas with several directed fisheries and aquacultures, while clawed lobsters are projected to shifts their envelope to northern latitudes likely affecting the North European, North American and Canadian fisheries. Fisheries represent an important resource for local and global economies and understanding how they might be affected by climate change scenarios is paramount when developing specific or regional management strategies.

2.2 Introduction

Climate change, overfishing and habitat degradation are the main reasons for the drastic decline of marine populations over the last 30 years (WWF, 2015). According to the United Nations Food and Agriculture Organization (FAO), one billion people, mostly in developing countries, depend directly on fish as their primary protein source. Fishing and aquaculture assure the livelihoods of 12% of the world’s population, creating economic benefits of USD $2.8 trillion per year (FAO, 2016). Yet, more must be done to understand and prepare for the impacts that climate change will have on world fisheries and marine ecosystems.

Coastal lobsters are a highly prized seafood delicacy all over the world and the crash of ground fish stocks prompted this industry to explode in some areas (Steneck & Wahle 2013). World lobster trade more than doubled over the last 20 years, with the global trade and production of lobster products adding up to over USD $8.4 billion worldwide (33% of the global trade; FAO (2016)). Nevertheless, the long larval phase of lobsters, particularly spiny *lobsters,* makes them particularly vulnerable to climate variability (Wahle *et al.*, 2015). Indeed, climate change effects have already been reported in several lobster stocks around the world mostly associated with ocean warming (e.g. Cockcroft *et al.,* 2008; Pecl *et al.,* 2009; Caputi *et al.,* 2010; Pinsky *et al.,* 2013; Wahle *et al.,* 2015; Rheuban *et al.,* 2017; Le Bris *et al.,* 2018).

Ecological Niche Models (ENM) have been widely used to assess the impacts of climate change on biodiversity (*e.g.* Albouy *et al.,* 2012; Jones & Chueng, 2015). These models combine distribution data of different species with environmental parameters to infer a specific bioclimatic envelope. Projecting this envelope under different climate scenarios allows an estimation of potential shifts in the habitat suitability of the species analysed (for review see Peterson *et al.* (2011)), allowing to infer on potential climate change impacts.

In this study we provide the first global forecast of changes in coastal lobster species distribution projected under climate change. Using an ensemble of ENMs (Thuiller *et al.,* 2009), we projected changes in richness for 125 coastal lobster species to an end-century stabilization scenario. We then compared our results with lobster fisheries data (as a proxy for human dependency on the resource) to help inform local fisheries and management strategies.

2.3 Methods

2.3.1 Species data

We obtained polygons of extent of occurrence (range filling) for 125 coastal lobster species from International Union for Conservation of Nature (IUCN, 2013) and converted them to presence point's data in a worldwide 1º x 1º latitude/longitude grid using ArcGIS (ESRI, 2006). Four families of decapod crustaceans commonly referred to as "lobsters" and associated with (but not restricted to) the continental shelf (200 m depth limit), were included in this analysis: 10 clawed lobsters species (family Nephropidae); 38 spiny lobsters species (family Palinuridae); 68 slipper lobsters species (family Scyllaridae) and 9 dwarf reef lobsters species (family Enoplometopodidae) (Supplementary material Table S01). To avoid statistical bias in ENM fitting, five species were excluded from the analyses (*Jasus caveorum, Jasus paulensis, Jasus tristani, Panulirus marginatus, Palinurus barbarae*) – corresponding to those with fewer than 20 records over the study area (Wisz *et al.,* 2008).

2.3.2 Climatic data

We used 30-year averages of five climate variables (sea surface temperature, sea surface salinity, total chlorophyll mass concentration at surface (proxy for productivity), dissolved oxygen concentration at surface and ocean surface pH) from Earth System Models (ESM) developed for CMIP5. There were 21 ESM's from 15 climate centres that modelled at least one of the variables analysed (Supplementary material Table S02). For each model and variable, we used the period 1976–2005 from the historical experiment, to establish the baseline period. And the period 2071–2100, to define our future scenario. A stabilization scenario was used in this study (Representative Concentration Pathway, RCP4.5), with CO2 concentrations projected to increase up to 650 ppm by 2100 (Vuuren *et al.,* 2011). This scenario was chosen as it's the one that projected the raise in surface temperature by the end-century closer to the +1,5ºC increase targeted by the Paris Agreement (UN, 2016), so we considered it the most realistic given the current status of international climate policy.

Climate data were publicly available from the World Climate Research Programme (*http://cmip-pcmdi.llnl.gov/cmip5/availability.html*). Sea surface temperature and surface seawater salinity have monthly frequency while the other three variables have annual data. All parameters were interpolated to the 1ºx1° grid used for the species in ArcGIS (ESRI, 2006), prior to calculating multi-model yearly means (Mora *et al.,* 2013). We estimated multi-model variability by calculating the standard deviation of model means among Earth System Models per variable and time period (Tebladi & Knutti, 2007; Supplementary material Fig. S01).

2.3.3 Ecological niche modelling

In order to constrain algorithmic uncertainty associated with Ecological Niche Models (ENM's) we implemented an ensemble forecasting method (Araújo & New 2007). Models were fitted using six different statistical techniques implemented in BioEnsembles (Diniz-Filho *et al.,* 2009): (1) BIOCLIM, (2) Euclidean distance (EUC), (3) Generalized Linear Models (GLM), (4) Generalized Additive Models (GAM), (5) Multivariate Adaptive Regression Splines (MARS), (6) Maximum Entropy (Maxent).

For each species, data were randomly partitioned into a calibration (70%) and a validation (30%) dataset, the procedure was repeated 5 times, maintaining the observed prevalence of species in each partition. For each species models optimal parameterization and fit evaluation were conducted using the True Skill Statistic (TSS) (Allouche *et al.,* 2006). Weighted median consensus forecasts were computed (Marmion *et al.,* 2009) and models performing poorly (with TSS values < 0.5) were excluded from the final ensemble (according to Landis & Koch, 1977 classification scheme). Consensus projections were built using 100% of the data, as data partitions have been shown to add significant uncertainty to forecasts (Araújo *et al.,* 2009). The final ensembles used performed at excellent levels with a mean TSS for all species of 0.83±0.09.

We restricted our analyses to the continental shelf (200 m depth limit), as species selected for the study are known to be strongly associated with this habitat (Phillips, 2013). Climate variables were only extracted for the superficial layer, as, given the coarse resolution of the climatic models used (Stock *et al.,* 2011) and the restricted depth range under study, we assumed that surface and benthic waters are included.

Once fitted the ecological niche models, species richness was computed for the baseline and future periods (for the whole coastal lobster assemblage and separately for its most relevant families—Fig. 1), summing the presences of species (per pixel) derived from a threshold of projected habitat suitability (HS). We then quantified the potential changes in species richness as the difference between future and baseline periods. Changes were also quantified for the genera with higher economic relevance within these families (*Panulirus, Jasus, Homarus* and *Nephrops* – Fig. 3), relating them with the global production per country for each genus (2016 data (ton); FAO (2016)). Data processing was performed using R (R Development Core Team, 2010) version 3.2.2.

2.4 Results

2.4.1 Present patterns in coastal lobster distribution

Richness for coastal lobster species was projected to peak around 14º S (mean HS 49 ± 11 species) and 9º N latitude (Fig. 1A - 37 ± 13 species) in the baseline period. When looking at the major coastal families, we find that spiny lobsters projected richness peak is around 18º S (13 ± 3 species), mostly due to diversity of the genera *Jasus* (Australia/New Zealand and South Africa areas) and *Panulirus* (Coral Triangle area), as well as around 9º N (11 ± 3 species), once again influenced by *Panulirus* species present on the wider Caribbean region (Fig. 1B). Clawed lobsters projected richness peaks around 17º S (3 ± 1 species), driven by the North Australian lobster diversity and 33º N (2 ± 1 species), mainly due to genera *Homarus* and *Nephrops* (Fig. 1C).

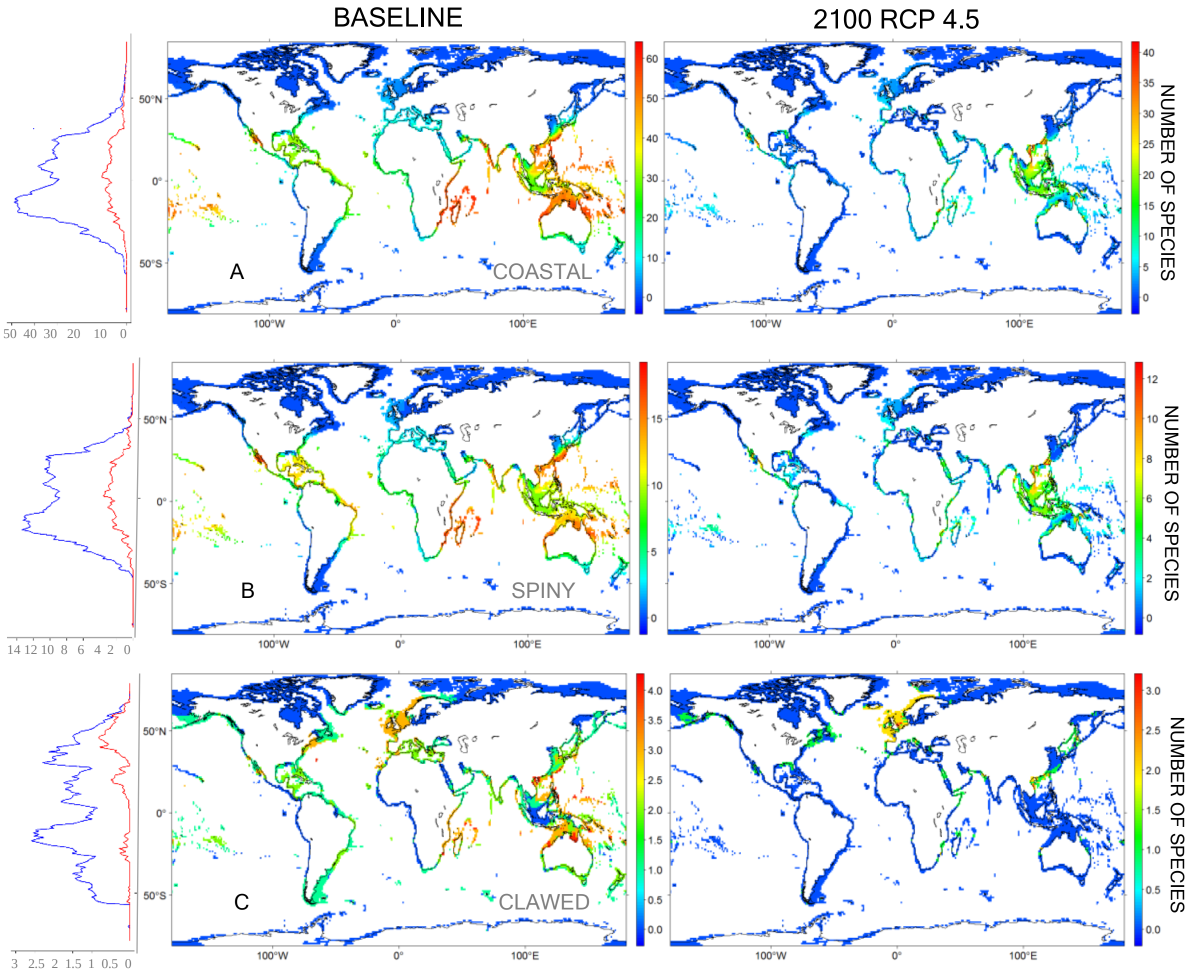

Fig. 1 Predicted species richness for A) coastal lobster species, B) spiny lobster and C) clawed lobster families, in the baseline and end-century periods according to the RCP 4.5 scenario. Left panel shows mean species richness predicted per latitude for the baseline period (blue line) and end-century (red line) scenario.

2.4.2 Projected changes in coastal lobster distribution

Projected losses in diversity for coastal lobster species occurred mainly in the tropical zone (between 18º S and 20º N), with species projected to contract their range between 40% and 100% (Fig. 2A). When looking at spiny lobsters (Fig. 2B), the main drivers of this trend, we project losses to be higher in the coasts of wider Caribbean region/Brazil, eastern Africa and Indo-Pacific area. As for clawed lobsters (Fig. 2C), our models project higher losses in the Mediterranean, East Africa and North Australia coasts.

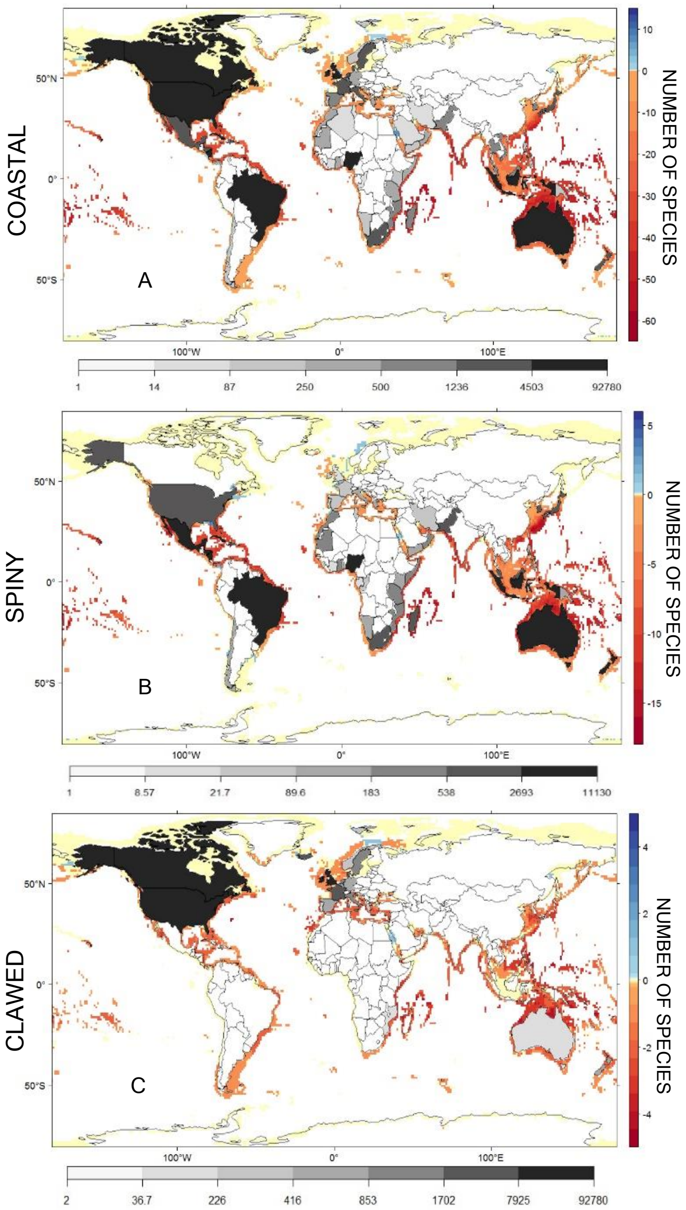

Fig. 2 Predicted changes in species richness for A) coastal lobster assemblage, B) spiny lobster and C) clawed lobster families, between baseline and end-century periods, under the RCP 4.5 scenario. In land shades of grey represent coastal lobster* global capture production per country [* see table S01 for species used; 2016 data (ton)].

Projected losses for spiny lobsters are highly related with the changes projected for genus *Panulirus* (Fig. 3A, a very speciose genus - 50% of spiny lobster species). Despite being less diverse, genus Jasus is also predicted to experience significant losses (between 92-100% range contraction) in areas as south Africa *(J. lalandii*), south Australia and New Zealand *(*J. *edwardsii)* coasts (Fig. 3B). Regarding clawed lobsters, our models project a range contraction of about *71% fo*r *H. americanus*, 44% for *H.*

gammarus and 58% for *N. norvegicus*, with all species projected to suffer a shift north and loss of HS in the southern range (Fig. 3 C-D).

2.5 Discussion

The projected pattern for higher diversity towards the tropics was strongly driven by the presence of diverse clades with tropical affinities (dwarf reef, slipper and some spiny lobster genera), but occurring at lower abundance when compared with the ones present in temperate waters [clawed and some spiny lobster genera; Phillips (2013)]. Our analyses provide a global picture of coastal lobster diversity and its distribution patterns.

Projected losses in suitable habitat for coastal lobster species occurred mainly in the tropical zone, with species projected to contract their climate envelope between 40 and 100%. Spiny lobsters higher losses are projected in the coasts of wider Caribbean region/Brazil, eastern Africa and Indo-Pacific area. These losses are driven by the projected changes for genus *Panulirus* and will likely have implications on the economy of affected countries. Since countries as Australia (4th world top lobster producer - 11 230 ton (65% from capture of Australian Spiny Lobster (*P. cygnus*)) and *Indonesia* (5th world top producer - 10 264 ton (98% capture exclusively from *Panulirus spp.*)) are highly dependent on these resources. Brazil, Bahamas (*P. argus*) and Nigeria are also in the top 10 world lobster producer capturing exclusively *Panulirus spp (Fig. 3A; FAO (2016)).* Despite being less diverse, genus Jasus is also predicted to experience significant range contractions in areas with profitable fisheries directed to this resource, as south Africa *(J. lalandii), south Australia and New* Zealand *(J. edwardsii*) coasts. On the other hand, farming of *P. ornatus (70%)* and *P. homarus* is blooming in the Indo-Pacific region [Indonesia, Vietnam, Malaysia and Philippines; Jones (2010)], revenuing USD $31 519 millions in *2016* (FAO, 2016). So it is crucial that potential changes in habitat suitability are considered when designing regional studies for management of stocks, development of new aquaculture ventures and design of protected areas.

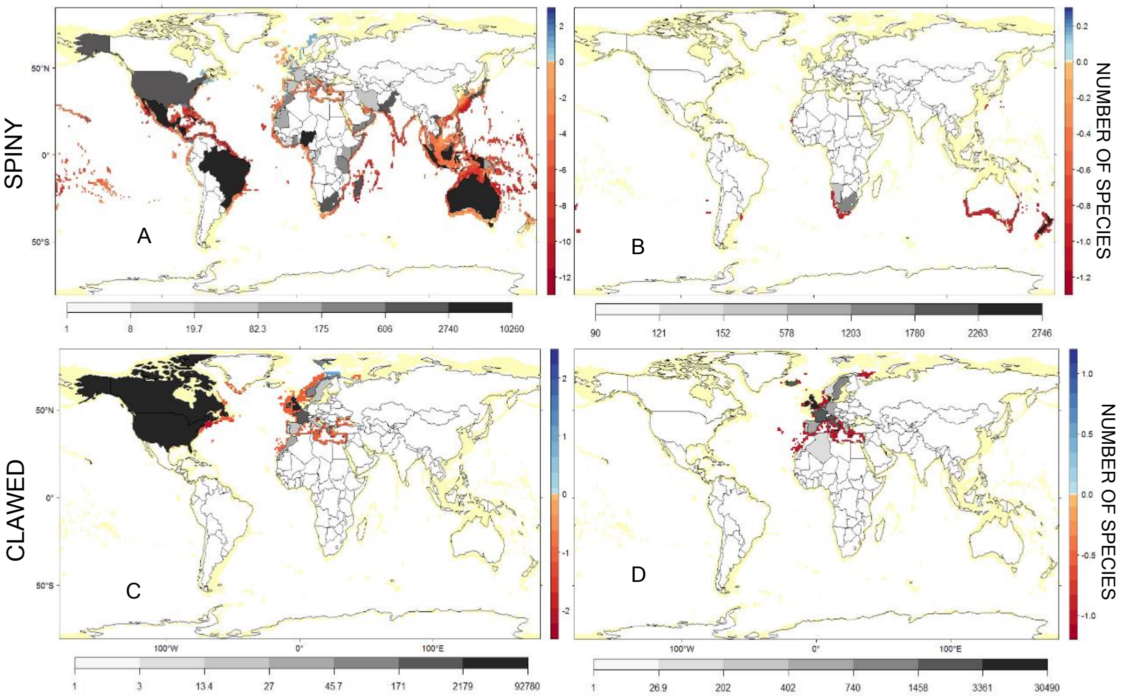

Fig. 3 Projected changes in species richness for the coastal lobster genera with commercial relevancy A) Panulirus, B) Jasus, C) Homarus and D) Nephrops) between the baseline and end-century periods, under RCP 4.5 scenario. In land shades of grey represent coastal lobster* global capture production per country [* see table S01 for species used; 2016 data (ton)].

Clawed lobsters are much less speciose, yet highly valuable, with only 3 species (*H. americanus* (52%), *H. gammarus* (3%) and *N. norvegicus* (19%)) being responsible for 74% of all world lobster production (Phillips, 2013; FAO, 2016). Both genera are restricted to temperate waters in the Northern hemisphere and are targeted by large commercial fisheries. Our models project significant envelope contraction, with all species projected to undergo a shift north and loss of suitable habitat in the southern range (Fig. 3 C-D). The projected envelope shifts and loss of suitable habitat will likely affect the North European, North American and Canadian fisheries with the potential of adverse effects on coastal communities' livelihood. Nevertheless recent studies using regional models with finer spatial resolution (Li *et al.,* 2018) showed that the strength of temperature effects on species distribution varied spatially in the Gulf of Maine area. These local or specific particularities are challenging to capture in a global study and results presented here should be considered at the coarse scale they were produced. Also, it's important to point out that even though our projections on habitat suitability loss may seem contradictory with other studies (e.g. Cheung *et al.,* 2009; Jones *et al.,* 2015), as they are projected not only for the tropics but also for higher latitudes (although with much less intensity). This can be easily explained by the use of climatic variables normally not included in other studies, as dissolved oxygen concentration at surface and ocean surface pH. It is long known that temperature is one of the climatic variable that better correlate with species distribution (Harley *et al.,* 2006), but factors like ocean acidification have proof to be equally detrimental, especially for crustaceans like lobsters, as they depend on carbonate to build their shells (Taylor *et al.,* 2015). In fact pH (and the interactions between the climatic variables) proved here to be a strong driver in coastal lobster species distribution and strongly influenced our projections, hence the loss of suitable habitat projected also at higher latitudes.

Model assumptions and limitations call for careful interpretation of the projected changes in species richness. First, the presented results relate to potential changes in HS, which build on the realized niche of the species that may or may not fully occupy their fundamental niche (for review see Peterson *et al.,* 2011). This means that the models can project potential losses in areas where the species does not occur at the present moment, but in terms of HS could potentially occur (e.g. Fig. 2D - potential loses are projected in the Mediterranean where *N. norvegicus* is not a coastal species). Second, as previously stated, the coarse resolution of the CMIP5 climate models limits the ability to predict finer processes affecting species distribution, such as stratification or variation in coastal currents that can significantly impact larval dispersal patterns (Caputi *et al.,* 2013). Recent high-resolution climate projections (Saba *et al.,* 2016) show a bias in global climate model simulations, indicating greater warming than projected by coarse resolution climate projections in some areas. Third, our model does not consider the potential for rapid evolutionary adaptation (Hofman & Sgrò, 2011) or migrations to greater depths (Dulvy *et al.,* 2008), which could help the species counter stressful climatic conditions. Despite these caveats, our results provide valuable inputs on the sensibility of different lobster species and geographical areas to climate change and guide when designing future assessments at a finer spatial or ecological scale (Caputi *et al.,* 2013).

2.6 References

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2.7 Supplementary material

Table S01 List of the 125 coastal lobster species used in this study, with their group and bathymetric range (min and max depth). Species marked with # are commercial fishing targets and with + are aquaculture productions.

SpId	Species	Family		Group	MinDepth	MaxDepth
sp_ 1	*Acantharctus ornatus*	Scyllaridae		Slipper	25	55
sp_ 2	*Acantharctus posteli*	Scyllaridae		Slipper	25	60
sp_ 3	*Antarctus mawsoni*	Scyllaridae		Slipper	80	540
sp_ 4	*Antipodarctus aoteanus*	Scyllaridae		Slipper	0	100
sp_ 5	*Arctides antipodarum*	Scyllaridae		Slipper	5	146
sp_ 6	*Arctides guineensis*	Scyllaridae		Slipper	0	400
sp_ 7	*Arctides regalis*	Scyllaridae		Slipper	5	50
sp_ 8	*Bathyarctus rubens*	Scyllaridae		Slipper	183	782
sp_ 9	*Biarctus pumilus*	Scyllaridae		Slipper	0	11
sp_ 10	*Biarctus sordidus*	Scyllaridae		Slipper	3	73
sp_ 11	*Biarctus vitiensis*	Scyllaridae		Slipper	6	48
sp_ 12	*Chelarctus aureus*	Scyllaridae		Slipper	100	200
sp_ 13	*Chelarctus cultrifer*	Scyllaridae		Slipper	124	300
sp_ 14	*Crenarctus bicuspidatus*	Scyllaridae		Slipper	2	108
sp_ 15	*Crenarctus crenatus*	Scyllaridae		Slipper	0	250
sp_ 16	*Eduarctus aesopius*	Scyllaridae		Slipper	16	33
sp_ 17	*Eduarctus lewinsohni*	Scyllaridae		Slipper	20	60
sp_ 18	*Eduarctus martensii*	Scyllaridae		Slipper	6	79
sp_ 19	*Eduarctus modestus*	Scyllaridae		Slipper	29	112
sp_ 20	*Eduarctus pyrrhonotus*	Scyllaridae		Slipper	33	71
sp_ 21	*Eduarctus reticulatus*	Scyllaridae		Slipper	33	72
sp_ 22	*Enoplometopus antillensis*	Enoplometopodidae		Dwarf Reef	5	201
sp_ 23	*Enoplometopus callistus*	Enoplometopodidae		Dwarf Reef	30	200
sp_ 24	*Enoplometopus crosnieri*	Enoplometopodidae		Dwarf Reef	80	120
sp_ 25	*Enoplometopus daumi*	Enoplometopodidae		Dwarf Reef	0	1
sp_ 26	*Enoplometopus debelius*	Enoplometopodidae		Dwarf Reef	12	25
sp_ 27	*Enoplometopus gracilipes*	Enoplometopodidae		Dwarf Reef	80	300
sp_ 28	*Enoplometopus holthuisi*	Enoplometopodidae		Dwarf Reef	20	80
sp_ 29	*Enoplometopus occidentalis*	Enoplometopodidae		Dwarf Reef	0	100
sp_ 30	*Enoplometopus voigtmanni*	Enoplometopodidae		Dwarf Reef	6	35
sp_ 31	*Evibacus princeps*	Scyllaridae		Slipper	2	90
sp_ 32	*Galearctus aurora*	Scyllaridae		Slipper	90	300
sp_ 33	*Galearctus kitanoviriosus*	Scyllaridae		Slipper	47	500
sp_ 34	*Galearctus timidus*	Scyllaridae		Slipper	80	390
sp_ 35	*Galearctus umbilicatus*	Scyllaridae		Slipper	70	230
sp_ 36	*Gibbularctus gibberosus*	Scyllaridae		Slipper	12	57
sp_ 37	*Homarinus capensis*	Nephropidae		Clawed	20	40

sp_ 38	*Homarus americanus #*	Nephropidae		Clawed	4	480
sp_ 39	*Homarus gammarus #*	Nephropidae		Clawed	0	150
sp_ 40	*Ibacus alticrenatus*	Scyllaridae		Slipper	20	455
sp_ 41	*Ibacus brevipes*	Scyllaridae		Slipper	186	457
sp_ 42	*Ibacus brucei*	Scyllaridae		Slipper	90	183
sp_ 43	*Ibacus chacei*	Scyllaridae		Slipper	2	330
sp_ 44	*Ibacus ciliatus #*	Scyllaridae		Slipper	49	314
sp_ 45	*Ibacus novemdentatus*	Scyllaridae		Slipper	37	400
sp_ 46	*Ibacus peronii*	Scyllaridae		Slipper	40	250
sp_ 47	*Ibacus pubescens*	Scyllaridae		Slipper	150	391
sp_ 48	*Jasus edwardsii #*	Palinuridae		Spiny	5	200
sp_ 49	*Jasus frontalis #*	Palinuridae		Spiny	2	200
sp_ 50	*Jasus lalandii #*	Palinuridae		Spiny	0	46
sp_ 51	*Justitia longimana*	Palinuridae		Spiny	1	300
sp_ 52	*Linuparus trigonus*	Palinuridae		Spiny	30	318
sp_ 53	*Metanephrops challengeri #*	Nephropidae		Clawed	140	640
sp_ 54	*Metanephrops mozambicus#*	Nephropidae		Clawed	180	750
sp_ 55	*Metanephrops rubellus*	Nephropidae		Clawed	50	150
sp_ 56	*Metanephrops taiwanicus*	Nephropidae		Clawed	50	500
sp_ 57	*Metanephrops thomsoni*	Nephropidae		Clawed	50	500
sp_ 58	*Nephrops norvegicus #*	Nephropidae		Clawed	20	800
sp_ 59	*Nephropsis aculeata*	Nephropidae		Clawed	137	824
sp_ 60	*Nupalirus chani*	Palinuridae		Spiny	150	340
sp_ 61	*Nupalirus japonicus*	Palinuridae		Spiny	40	200
sp_ 62	*Nupalirus vericeli*	Palinuridae		Spiny	160	320
sp_ 63	*Palinurellus gundlachi*	Palinuridae		Spiny	2	35
sp_ 64	*Palinurellus wieneckii*	Palinuridae		Spiny	9	27
sp_ 65	*Palinurus charlestoni*	Palinuridae		Spiny	50	300
sp_ 66	*Palinurus delagoae #*	Palinuridae		Spiny	0	400
sp_ 67	*Palinurus elephas #*	Palinuridae		Spiny	5	160
sp_ 68	*Palinurus gilchristi #*	Palinuridae		Spiny	55	360
sp_ 69	*Palinurus mauritanicus #*	Palinuridae		Spiny	180	400
sp_ 70	*Palinustus mossambicus*	Palinuridae		Spiny	59	406
sp_ 71	*Palinustus truncatus*	Palinuridae		Spiny	120	298
sp_ 72	*Palinustus waguensis*	Palinuridae		Spiny	72	84
sp_ 73	*Panulirus argus #*	Palinuridae		Spiny	0	90
sp_ 74	*Panulirus cygnus #*	Palinuridae		Spiny	0	120
sp_ 75	*Panulirus echinatus*	Palinuridae		Spiny	0	35
sp_ 76	*Panulirus femoristriga*	Palinuridae		Spiny	0	20
sp_ 77	*Panulirus gracilis #*	Palinuridae		Spiny	0	18
sp_ 78	*Panulirus guttatus*	Palinuridae		Spiny	2	23
sp_ 79	*Panulirus homarus # +*	Palinuridae		Spiny	1	90
sp_ 80	*Panulirus inflatus*	Palinuridae		Spiny	0	30
sp_ 81	*Panulirus interruptus*	Palinuridae		Spiny	0	65
sp_ 82	*Panulirus japonicus*	Palinuridae		Spiny	1	15

sp_ 83	*Panulirus laevicauda*	Palinuridae		Spiny	0	50
sp_ 84	*Panulirus longipes #*	Palinuridae		Spiny	1	18
sp_ 85	*Panulirus ornatus # +*	Palinuridae		Spiny	1	18
sp_ 86	*Panulirus pascuensis*	Palinuridae		Spiny	0	5
sp_ 87	*Panulirus penicillatus*	Palinuridae		Spiny	1	4
sp_ 88	*Panulirus polyphagus*	Palinuridae		Spiny	3	90
sp_ 89	*Panulirus regius*	Palinuridae		Spiny	1	40
sp_ 90	*Panulirus stimpsoni*	Palinuridae		Spiny	0	40
sp_ 91	*Panulirus versicolor*	Palinuridae		Spiny	1	15
sp_ 92	*Parribacus antarcticus*	Scyllaridae		Slipper	0	20
sp_ 93	*Parribacus caledonicus*	Scyllaridae		Slipper	0	6
sp_ 94	*Parribacus japonicus*	Scyllaridae		Slipper	1	20
sp_ 95	*Parribacus scarlatinus*	Scyllaridae		Slipper	0	20
sp_ 96	*Petrarctus brevicornis*	Scyllaridae		Slipper	60	150
sp_ 97	*Petrarctus demani*	Scyllaridae		Slipper	5	59
sp_ 98	*Petrarctus holthuisi*	Scyllaridae		Slipper	80	300
sp_ 99	*Petrarctus rugosus*	Scyllaridae		Slipper	20	200
sp_ 100	*Remiarctus bertholdii*	Scyllaridae		Slipper	15	150
sp_ 101	*Sagmariasus verreauxi*	Palinuridae		Spiny	0	155
sp_ 102	*Scammarctus batei*	Scyllaridae		Slipper	160	484
sp_ 103	*Scyllarides aequinoctialis*	Scyllaridae		Slipper	0	180
sp_ 104	*Scyllarides astori*	Scyllaridae		Slipper	10	50
sp_ 105	*Scyllarides deceptor*	Scyllaridae		Slipper	45	200
sp_ 106	*Scyllarides delfosi*	Scyllaridae		Slipper	2	91
sp_ 107	*Scyllarides elisabethae*	Scyllaridae		Slipper	37	380
sp_ 108	*Scyllarides haanii*	Scyllaridae		Slipper	10	135
sp_ 109	*Scyllarides herklotsii*	Scyllaridae		Slipper	10	300
sp_ 110	*Scyllarides latus #*	Scyllaridae		Slipper	4	100
sp_ 111	*Scyllarides nodifer*	Scyllaridae		Slipper	2	91
sp_ 112	*Scyllarides squammosus*	Scyllaridae		Slipper	20	80
sp_ 113	*Scyllarides tridacnophaga*	Scyllaridae		Slipper	5	112
sp_ 114	*Scyllarus americanus*	Scyllaridae		Slipper	5	21
sp_ 115	*Scyllarus arctus*	Scyllaridae		Slipper	4	50
sp_ 116	*Scyllarus caparti*	Scyllaridae		Slipper	25	55
sp_ 117	*Scyllarus depressus*	Scyllaridae		Slipper	29	422
sp_ 118	*Scyllarus paradoxus*	Scyllaridae		Slipper	22	29
sp_ 119	*Scyllarus planorbis*	Scyllaridae		Slipper	18	99
sp_ 120	*Scyllarus pygmaeus*	Scyllaridae		Slipper	5	100
sp_ 121	*Scyllarus subarctus*	Scyllaridae		Slipper	100	300
sp_ 122	*Thenus australiensis*	Scyllaridae		Slipper	9	85
sp_ 123	*Thenus indicus*	Scyllaridae		Slipper	10	30
sp_ 124	*Thenus orientalis #*	Scyllaridae		Slipper	8	100
sp_ 125	*Thenus parindicus*	Scyllaridae		Slipper	7	84

Table S02 The table shows the list of Earth System Models used for each variable analysed. We considered only models that provided the complete series of data from 1860 to 2100 under the historical and RCP 4.5 experiment. The variables analysed included sea surface temperature (CMIP5 variable name ‘TOS’, in K (converted to ºC in this study)), sea surface salinity (‘SOS’, in psu), total chlorophyll mass concentration at surface (‘Chl’, in kg m^{-3}), dissolved oxygen concentration at surface (‘O_2’, in mol m^{-3}) and pH at surface (‘pH’, in mol H kg^{-1}).

MODELLING CENTER	COUNTRY	MODEL	Chl	O_2	pH	SOS	TOS
BCC	China	BCC-CSM1-1					x
		BCC-CSM1-1-m					x
CCCma	Canada	CanESM2	x		x	x	x
NCAR	USA	CCSM4				x	x
NSF-DOE-NCAR	USA	CESM1(CAM5)				x	x
CNRM-CERFACS	France	CNRM-CM5	x	x	x	x	x
CSIRO-QCCCE	Australia	CSIRO-Mk3.6.0				x	x
FIO	China	FIO-ESM					x
NOAA GFDL	USA	GFDL-CM3				x	x
NASA GISS	USA	GISS-E2-H				x	x
		GISS-E2-R				x	x
MOHC	UK	HadGEM2-AO				x	x
		HadGEM2-ES	x	x		x	x
IPSL	France	IPSL-CM5A-LR	x	x	x	x	x
MIROC	Japan	MIROC5				x	x
		MIROC-ESM	x		x	x	x
		MIROC-ESM-CHEM	x		x	x	x
MPI-M	Germany	MPI-ESM-LR	x	x	x	x	x
		MPI-ESM-MR	x	x	x	x	x
MRI	Japan	MRI-CGCM3					x
NCC	Norway	NorESM1-M				x	x
TOTAL MODELS			8	5	7	17	21

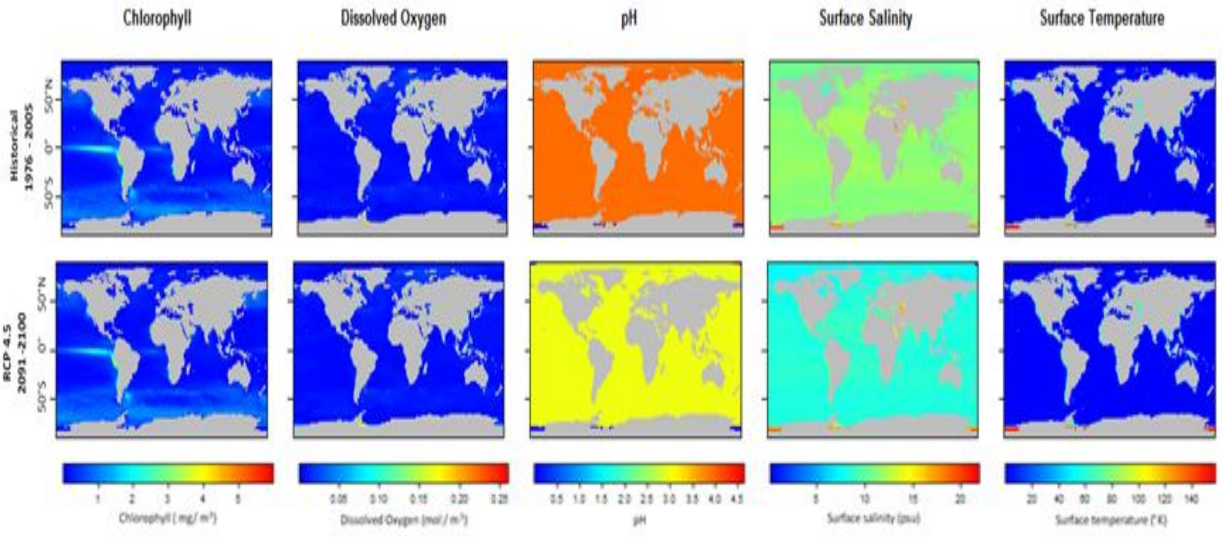

Fig. S01 Multi-model mean Standard Deviation across model means per scenario and time period as a measure of precision.

CHAPTER 3

3. GLOBAL PATTERNS OF CEPHALOPOD COASTAL DIVERSITY UNDER CLIMATE CHANGE

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3. GLOBAL PATTERNS OF CEPHALOPOD COASTAL DIVERSITY UNDER CLIMATE CHANGE

3.1 Abstract

Coastal marine systems are currently being exposed to climate change at a much faster rate than many other ecosystem, with coastal species being exposed to several stressful factors. Cephalopod mollusks play a pivotal role in marine trophic webs, and most are ‘keystone’ species owing to their influence on ecosystem dynamics. Here, we characterize the global patterns of coastal cephalopod diversity and present, for the first time, a global forecast of potential changes in richness, mean body size and assemblage composition (i.e., species replacement, nestedness, and combinations of both) for 161 coastal cephalopod species under climate change, using an ensemble of ecological niche models (ENMs) for an end of the century mitigation scenario. We show that for the baseline period, coastal cephalopod diversity is higher in the Central Indo-Pacific area and that body size patterns follows the temperature-size rule, with larger animals occurring at higher latitudes. End-century projections of habitat suitability show a different picture, with 96% of cephalopod species predicted to experience range contraction and 15% completing losing their environmental space. Nestedness is projected to be the main driver of species compositional change. Maximum body size is projected to increase in 44% of the pixels and decrease in 37%. Regarding fisheries, the projected changes are more favorable to the countries at higher latitudes, although the search of refugia of smaller tropical species might potentially lead to a mitigation of the negative effects of climate change in these areas, as measured by the total capture (ton). Despite models limitation our findings reflect major climatic drivers of change and highlight the idea that even though cephalopod species seem good candidates to replace overexploited fish stocks in the near future, they may not have the environmental space to do so.

3.2 Introduction

Climate change scenarios predict global sea surface temperature (SST) to rise globally throughout the 21st century (IPCC, 2013) and marine biota is expected to respond to this warming trend by shifting their geographical (Pinsky *et al.*, 2013; Jones & Cheung, 2014) and bathymetric ranges (Dulvy *et al.*, 2008). Coastal marine systems are currently being exposed to warming at a much faster rate than many other ecosystems (Harley *et al.*, 2006) and as several species already live close to their thermal tolerance limits (Rosa *et al.*, 2014), an increase in extinction rates of many marine organisms is expected (Lasram *et al.*, 2010).

Cephalopods are invertebrates known to play an important ecological role in marine trophic webs (both as prey and as predators) and are commonly defined as 'keystone' species owing to their strong influence on ecosystem dynamics (Rosa *et al.*, 2013a, b). Thus, changes in cephalopod abundance can have a mixed impact on marine communities and fisheries, contributing to changes in their predators and prey abundance (André *et al.*, 2010). In addition, given their short lifespans and rapid growth rates, cephalopods are expected to respond faster than other marine species to changes in environmental conditions, making them good indicators of environmental change (Pierce *et al.*, 2010). It is also important to note that these mollusks are a significantly growing component of global fisheries, with landings increasing steadily from the 1950s to reach about four million tons annually over the last decade (Doubleday *et al.*, 2016).

Marine fisheries productivity is likely to be affected by the alteration of ocean conditions including water temperature, ocean currents and coastal upwelling, as a result of climate change (*e.g.* Lam *et al.,* 2016; IPCC, 2014). Such changes in ocean conditions may affect primary productivity, species distribution, community and food web structure that have direct and indirect impacts on the goods and services provided by marine ecosystems, which will have direct implication for the welfare of human society (FAO, 2018)

A central question in studies exploring the effects of climate change on biodiversity is how changes are going to be measured and characterized. We can assume that species respond individualistically to environmental changes and model distributions of individual species one at a time (Guissan & Thuiller, 2005). Or that the distribution of species can potentially be influenced by the distribution of other taxa, using community-level modelling strategies instead (Gotelli *et al.,* 2010). Beta diversity describe the extent of compositional change in the community between sites and also attempt to reveal the assembly mechanisms that drive these differences (Bishop *et al.,* 2015). Most studies examine species temporal turnover (*e.g*. Hillebrand *et al.*, 2010; Poloczanska *et al.,* 2013; ,Cheung *et al.*, 2015; Pecl et al., 2017; Lotze *et al.,* 2019) but frameworks exist to assess changes in species turnover both in time and space (e.g. Almeida-Neto *et al.*, 2011; Baselga, 2012). Species Temporal Turnover (STT) is a widely used metric to assess these changes in composition (e.g. Almeida-Neto et al., 2011; Baselga, 2012). However, as a measure of beta diversity equivalent to the Jaccard dissimilarity index (Anderson *et al.*, 2011), it mixes two components in one metric: changes in assemblage composition caused by a process of species loss or gain (i.e., the nestedness component of beta diversity); and changes in assemblage composition caused by a process of species replacement (i.e. the pure turnover component of beta diversity). Following Baselga (2010,2012), Albouy *et al.* (2012a) proposed a strategy to fully apprehend the potential effects of climate change on species assemblages by analyzing changes in species richness and changes in species composition together, and highlighted a bivariate mapping strategy to picture simultaneously the spatio-temporal trend of both processes.

Beyond species composition, another important issue is how to account for functional and phenotypic differences in multispecies assemblages. Quantifying the distribution of traits in a community or the relative magnitude of species similarities can give us a good measure of the assemblage functional diversity (Cadotte *et al.,* 2011). Body size is considered a fundamental species trait and a good indicator of ecosystem functioning because of its relationship to several functional traits such as growth, reproduction and mortality (Brown *et al.*, 2004). Also body size is an easy and cheap way to translate several co-varying traits into a single one (Woodward *et al.*, 2005). Commercial fishing is known to constrain body size distributions of marine populations, as most fishing gear is size selective and targets preferentially large bodied organisms (Myers & Worm, 2003). The increased temperatures associated with climate change are expected to disrupt large scale patterns in body size distributions (Sheridan & Bickford, 2011; Cheung *et al.*, 2012) and ecosystem functioning (Fisher *et al.*, 2010). Still the effect of climate change on marine populations is less studied than the effects of fishing, so large scale projections of climate mediated changes in body size distribution are urgent.

In this study we provide the first forecast of global changes in coastal cephalopod species richness projected under climate change. Using an ensemble of ecological niche models (*e.g*. Diniz-Filho *et al.*, 2009) we projected changes in habitat suitability for 161 coastal cephalopod species to an end-century stabilization scenario. We then examined how spatial and temporal components of coastal cephalopod assemblage diversity are projected to change toward the end of the century. Lastly, we inferred the potential effects in body size distributions and its potential impacts in global cephalopod fisheries.

3.3 Material and Methods

3.3.1. Species and climate data

We obtained polygons of extent of occurrence (range filling) for 161 coastal cephalopod species (79 cuttlefishes, 71 squids and 10 octopus species; see list of species in Table S01) from Food and Agriculture Organization of the United Nations (FAO) (Jereb & Roper, 2005, 2010; Jereb *et al.*, 2016) and converted them to presence points data in a 1º x 1º latitude/longitude grid using ArcGIS (ESRI, 2006). To avoid statistical bias in ENM fitting, 5 species were excluded from the analyses – corresponding to those with fewer than 20 records over the study area (Wisz *et al.*, 2008).

Patterns of marine species distribution are strongly influenced by bathymetry (Dambach & Roedder, 2011), so in order to reduce false positives in the presence data we refined the extent of occurrence maps by clipping off areas with depths falling outside the bathymetric range of the species (Jereb & Roper, 2005, 2010). The bathymetry of the ocean was obtained from ETOPO2 (2010) and resampled to a 1º x 1º latitude/longitude grid. We also restricted analyses to species associated with, but not restricted to, the continental shelf (200 m depth limit), since they are more likely to be affected by climate change (Rosa *et al.*, 2012b).

We used 30-year averages of five climate variables (sea surface temperature, sea surface salinity, total chlorophyll mass concentration at surface, dissolved oxygen concentration at surface and ocean surface pH) from Earth System Models (ESM) developed for CMIP5. There were 21 ESM's from 15 climate centres in 9 countries that modelled at least one of the variables analysed (Table S02). For each model and variable, we used the period 1976–2005 from the historical experiment, to establish the baseline period. And the period 2071–2100, to define our future scenarios. A stabilization scenario was used in this study (Representative Concentration Pathway, RCP4.5), with CO2 concentrations projected to increase up to 650 ppm by 2100 (Vuuren *et al.,* 2011). This scenario was chosen as it's the one that projected the raise in surface temperature by the end-century closer to the +1,5ºC increase targeted by the Paris Agreement (Nations, 2016), so we considered it the most realistic at the present moment.

Climate data were publicly available from the World Climate Research Programme (http://cmip-pcmdi.llnl.gov/cmip5/availability.html). Sea surface temperature and surface seawater salinity have monthly frequency while the other three variables have annual data. We only extracted the first layer (i.e., surface) for chlorophyll, dissolved oxygen, and pH. All parameters were interpolated into a common 1° by 1° grid prior to calculating multi-model means (Mora *et al.*, 2013). We estimated multi-model variability by calculating the standard deviation of model means among Earth System Models per variable and time period (Figure S01). There are several methods to ensemble ESM's, but average of several coupled climate models is usually found to agree better with observations than any single model (Tebaldi & Knutti, 2007).

To determine the extent of environmental differences between baseline and future climates a Multivariate Environmental Similarity Surfaces (MESS) analyse was performed, as proposed by Elith *et al.* (2010). For each cell, the degree of similarity between the new environments and those in the baseline period was computed (negative values represent dissimilarity). As models are less reliable when predicting outside their domain (Barbosa *et al.*, 2009), we have to carefully interpret the results for those areas. These calculations were performed using the modEvA R package [Figure S02 - Barbosa *et al.*, 2014)].

To match the resolutions of species and climate data, all datasets were re-sampled in ArcGIS (ESRI, 2006) to the 1° grid used for species. Data processing and statistical analyses were performed using R software (R Development Core Team, 2010).

3.3.2. Ecological niche models

In order to constrain algorithmic uncertainty associated with Ecological Niche Models (ENM's) we implemented an ensemble forecasting method (Araújo & New, 2007). Models were fitted using seven different modelling techniques implemented in BioEnsembles (Diniz-Filho *et al.*, 2009): (1) BIOCLIM, (2) Genetic Algorithm for Rule-Set Prediction (GARP), (3) Generalized Linear Models (GLM), (4) Generalized Additive Models (GAM), (5) Multivariate Adaptive Regression Splines (MARS), (6) Maximum Entropy (Maxent), (7) Neural Network (NNET).

For each species, data were randomly partitioned into calibration (75%) and validation (25%) dataset, the procedure was repeated 5 times, maintaining the observed prevalence of species in each partition, and models for each species were fit and evaluated using the True Skill Statistic (TSS) (Allouche *et al.*, 2006). Weighted median consensus forecasts were computed (Marmion *et al.*, 2009) and models performing poorly (with TSS values ≤ 0.5) were excluded from the final ensemble (according to Landis & Koch, 1977 classification scheme). Consensus projections were built using 100% of the data, as data partitions have been shown to add significant uncertainty to forecasts (Araújo *et al.*, 2009).

Using projected future climatic conditions we estimated changes in the geographic location of environmental niches for each species. We imposed some limitations to dispersal, as we considered unrealistic for a cephalopod species (or larvae) to move beyond important geographical barriers or disperse across major oceans to reach climatically suitable areas. So we used an adapted version of Spalding *et al.* (2007) ecoregions and only allowed species to move to an adjacent realm between time periods (Figure S03 shows the realms used in this study). We also imposed bathymetric limitations so that species would not be allowed to colonise a cell if it fell outside the species' bathymetric range (Albouy *et al.*, 2012b).

We calculated each species potential distributions for each time period, and calculated coastal cephalopod diversity by stacking individual distributional maps on the top of each other and infer species richness in each grid cell. We projected diversity for coastal cephalopods as a whole and individually for its three main groups - cuttlefishes, squids, octopuses. We then quantified the potential changes in cephalopod species richness as the difference between the future and the baseline period.

Then, we analysed potential changes in cephalopod assemblage composition (species replacement vs. nestedness) between the two time periods. Using Species Temporal Turnover (SST; as described in Albouy *et al.*, 2012a) and its decomposition, we chose Beta ratio (βratio) as a useful index to describe the relative contribution of each component (species replacement vs. nestedness) in the overall amount of STT. βratio values smaller than 0.5 indicate that species replacement is the main driver of STT, whereas values greater than 0.5 indicate that STT is mostly caused by nestedness (if βratio=1 - nestedness is the sole driver of STT; βratio=0 – only replacement explains STT). Here, we determined βratio as the ratio between the nestedness component of the Jaccard's dissimilarity index (βjne) and Jaccard's dissimilarity index (βjac) (Dobrovolski *et al.*, 2011).

We also project changes in the distribution of mean body size of assemblages using measurements of species maximum body size provided by FAO (Jereb & Roper, 2005, 2010; Jereb *et al.*, 2016), by comparing current and projected future distributions of mean body size, under climate change. To limit the effect of extremely large body sizes and account for non-normal distributions we used the logarithm of body size and applied the geometric rather than the arithmetic mean (Fisher *et al.*, 2010). Body size analyses were averaged at the level of Exclusive Economic Zones (EEZ), so they can relate with the potential economic impacts of climate change on cephalopod fisheries (cephalopod global capture production per country (FAO, 2016) was used as proxy for countries dependency on resource).

In addition, we quantified the potential effect of climate change on species range sizes by calculating the relative loss or gain (0.5 threshold in probability of occurrence) of the potential geographic ranges sizes (measured as number of cells occupied by a species) between the future and baseline period.

3.4 Results

3.4.1. Model prediction accuracy and environmental variables importance

The predictive accuracy of the seven ENM´s used in this analyses was classified from ‘fair’ to ‘excellent’ (according to Landis & Koch, 1977 classification scheme), with a mean TSS criterion of 0.69±0.08. The model with the lowest TSS was GARP (TSS=0.45±0.34) and the highest TSS was obtained with GAM, with TSS=0.84±0.09. Final ensembles performed at ‘excellent’ levels with a TSS of 0.81±0.11.

pH was the environmental variable responsible for an higher percentage (55%) of new environmental space, chlorophyll was 21% of the area, sea surface temperature was in 13%, oxygen in 8% and sea surface salinity in 3%.

3.4.2. Cephalopod hotspots and projected changes in richness

The zeniths of coastal cephalopod diversity for the baseline period, were projected in the Western/Central Indo-Pacific area, with a mean richness of 39±15 species at 8ºN latitude and 38±13 species at 9.5º S (Fig. 1A). When looking at the major coastal cephalopod families, we project a cuttlefishes richness hotspot around 12º N (19±8 species), in the Bay of Bengal area (Fig. 1C). Squids projected diversity peaks around 7.5ºS (19±4 species), in the central Indo-Pacific (Fig. 1E). Finally, Octopus diversity zeniths are projected around 40ºN (3±2 species) in the Mediterranean Sea and around 17ºN (2±1 species) on the wider Caribbean region (Fig. 1G).

Hotspots in the future scenario are projected to shift toward higher latitudes and present less diverse assemblages. Future coastal cephalopod richness zeniths are projected around 21ºN latitude (Fig. 1B; 13±11 species), at the Bay of Bengal and the China Sea area and around 18ºS (13±6 species) in the Madagascar coast area. This latitudinal patterns are driven mostly by the cuttlefishes (Fig. 1D; zeniths at 21ºN (5±6 species) and 19.5ºS latitudes (4±3 species)) and squids (zeniths at 20ºN (8±5 species) and 18ºS latitudes (8±3 species)) diversity, despite this last group present a high diversity all throughout the Indo-Pacific area (Fig. 1F; zenith around 1ºS (8±5 species)). Octopus hotspots are projected to slightly shift North, but remaining in the same areas (Mediterranean Sea and Caribbean region), still they are projected to suffer a threefold decrease in richness (Fig. 1H).

By the end-of-century, 69% of the continental shelf is predicted to experience some loss in adequate environmental niches, whereas only 12% is predicted to gain (Fig. 2 – right panels). Habitat loss for coastal cephalopods is predicted to occur mostly in the tropics, with peaks at 10.5ºS and 8ºN latitudes, with a mean loss up to 39±15 species. The gains in habitat are predicted only for the northern latitudes above 70ºN, but with much less intensity than losses (1±1 species).

Under the future climate change scenario the potential geographic range sizes of coastal cephalopods are projected to decrease for 149 species (95%), of which 24 (15%) are projected to completely lose their suitable environmental space and increase only for 7 species (5%). The same trend is true for the main groups within the cephalopod class, with the cuttlefishes shrinking their potential range in 95% of the species (with 15% projected to completely losing their suitable habitat), the squids in 96% of the species (of which 14% are projected to disappear) and in the octopuses 100% of the species are projected to reduce geographic range (with 30% projected to completely lose adequate environment).

3.4.3. Projected changes in cephalopod composition

Nestedness contributed more than replacement in explaining the temporal pattern of cephalopod turnover (Fig. 2B, mean βratio= 0.64±0.41). It was also the key contributor to the total amount of Species Temporal Turnover (STT) in 48% of cells (mean βratio= 0.95±0.13).

Predominant replacement was only verified in 32% of cells (mean βratio= 0.13±0.14). For the remaining cells in the continental shelf, the βratio was not calculated since there were no changes in predicted habitat suitability for all occurring species between periods. When looking at the latitudinal patterns of STT, replacement is more intense in the northern latitudes, above 50ºN, with squids being the main driver of this pattern. In all the remaining latitudes nestedness is the main driver of turnover, with the highest values in the equatorial latitudes, driven both by cuttlefishes and squids patterns (Fig. 2 – left panels).

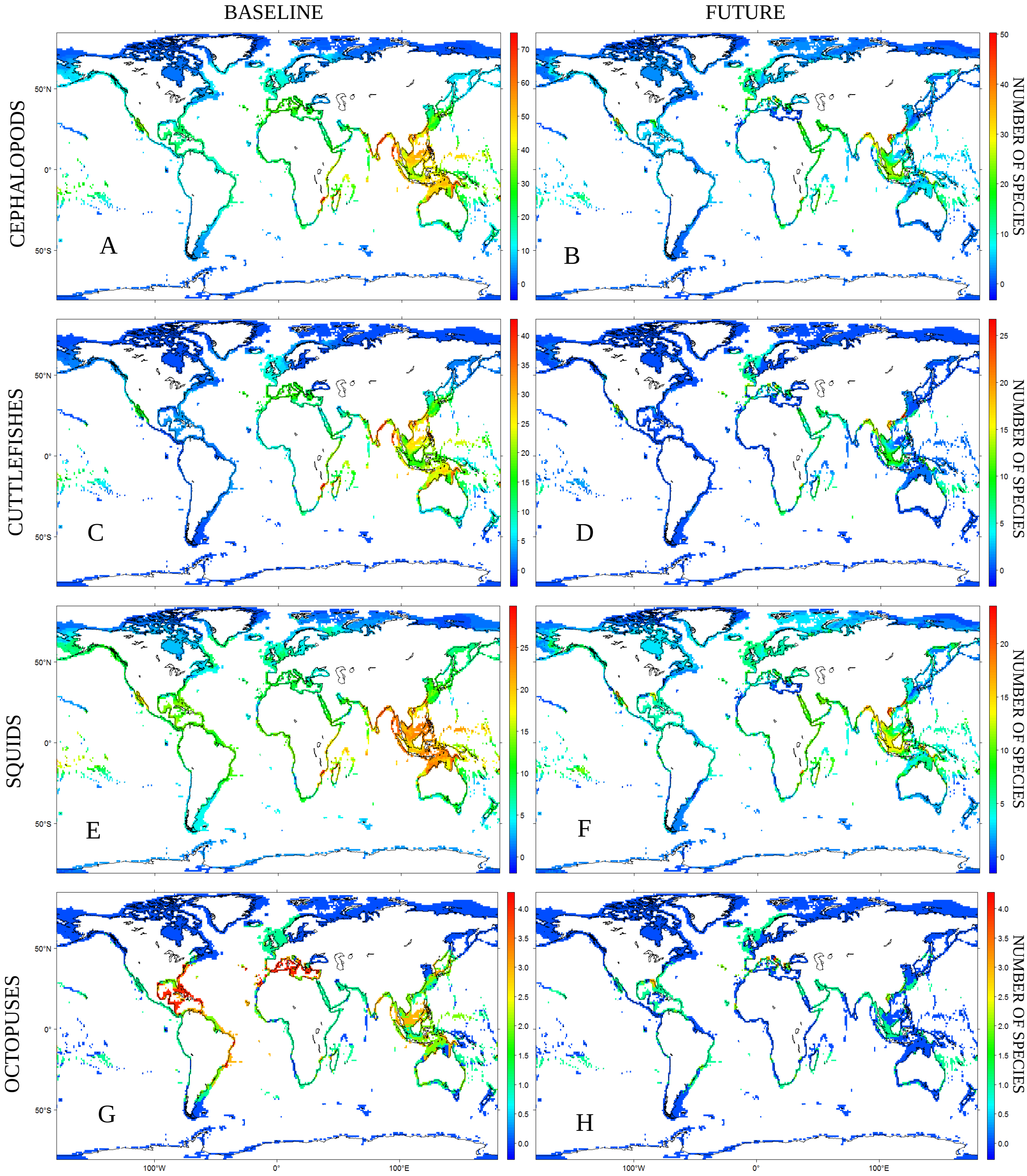

Fig.1 Projected richness for the baseline and the end-of-century period, under IPCC AR5 RCP4.5 scenario, for coastal cephalopods and its main groups (cuttlefishes (n=76), squids (n=69), octopuses (n=11)).

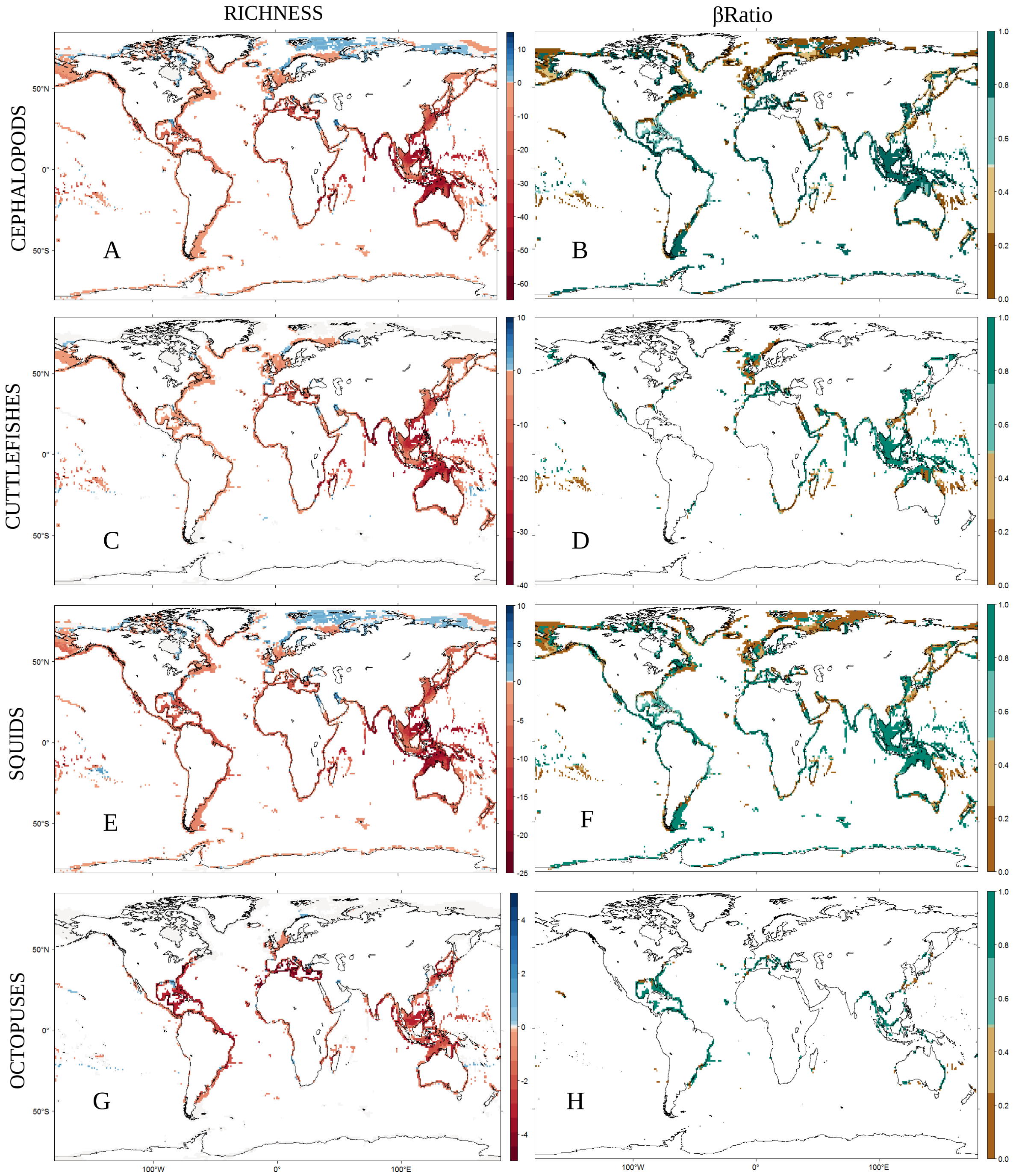

Fig. 2 Predicted changes in richness and composition between the baseline and the end-of-century period, under IPCC AR5 RCP4.5 scenario, for the coastal cephalopods assemblages. Changes in diversity are quantified using delta richness (DRS) and changes in composition using the βratio index.

3.4.4 Current patterns and projected changes in body size distributions

Species body size patterns in the baseline scenario presents a general trend of higher values towards higher latitudes, with a maximum mean body size of 5.91±0.26 (log) cm around 53ºS. Our models project decrease in maximum mean body size to occur in 37%

of the globe, mainly in the higher latitudes above 50ºN, and to increase in 44%, mostly in the intermediate latitudes (between 50ºN and 30ºS). Some of the areas projected to suffer a reduction in maximum mean body size are located near countries with higher dependency on the resource (e.g. Russia, EUA, Chile, Italy).

3.5 Discussion

Here we provide a first attempt to understand the global patterns of cephalopod diversity within the neritic realm and explore changes projected to happen due to climate change. We show that the hotspot of coastal cephalopod richness is found in the Central Indo-Pacific region, particularly in the East China Sea and in the Eastern Philippines ecoregions (Fig. 1 – left panels). Given the limiting number of Octopus occurrence data obtained for this study (10 species), it might seem that this coastal cephalopods hotspot is driven mainly by the high diversity of squids and cuttlefish, nevertheless this may not be true as is known that many Octopus species are endemic in this region (Jereb *et al.*, 2016). The Central Indo-pacific region is described as a biodiversity hotspot for many marine taxa (Roberts *et al.*, 2002; Tittensor *et al.*, 2010) and several authors have suggested different hypotheses, based on particularly rich environmental conditions or historical geological events, that might have promoted speciation processes and/or refuge in this area (Renema *et al.*, 2008; Cowman & Bellwood, 2013; Leprieur et al., 2016), explaining the high marine diversity found in the Central Indo-Pacific region. Our projections are in line with the results of a recent study (Rosa *et al.,* 2019) exploring for the first time the global patterns of species richness in coastal cephalopods, showing that despite the lack of data for some groups (*e.g.* octopus) our models provide a good picture of the current global patterns.

Regarding changes in cephalopod diversity, we found that projected losses of habitat suitability for species were more important within the tropical areas whereas gains were greater towards the poles (Fig. 2 – right panels). These findings are consistent with studies that revealed poleward shifts in species distribution within the 20th century (*e.g.* Burrows *et al.*, 2011; Poloczanska *et al.*, 2013), as well as predictions of shifts in the 21t century (*e.g.* Pereira *et al.*, 2010; Jones & Cheung, 2014). In the tropics, marine animals tend to have their critical thermal tolerances close to environmental temperature limits

(Tewksbury *et al.*, 2008), making them highly sensitive to warmer temperatures. In terrestrial organisms, physiological adaptation to heat seems to be generally impaired (Araújo *et al.*, 2013), although this patterns has not been fully explored in marine environments. Should the pattern be true for marine organisms, then moving to cooler habitats at higher latitudes would constitute the more viable adaptive strategy. Another alternative is for animals to seek deeper colder water in response to environmental warming (Dulvy *et al.*, 2008) However, moving towards the deep ocean might be unsuitable for coastal cephalopods, since most of them are highly dependent on the complexity and diversity of neritic habitats for reproduction (Boyle & Rodhouse, 2005).

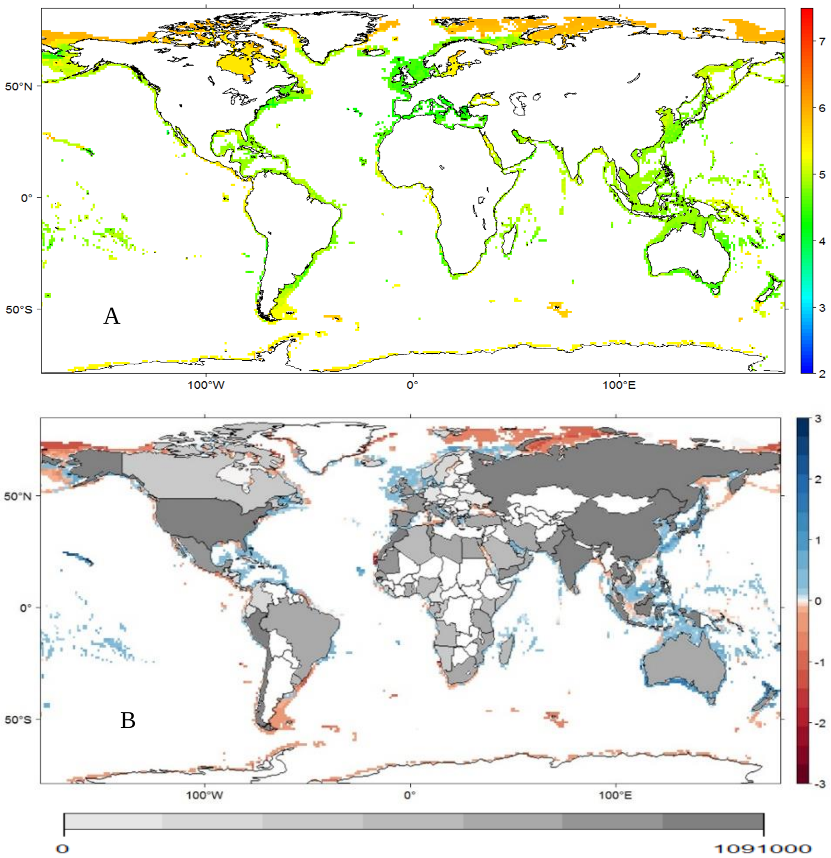

Fig. 3 A) Distribution of geometric mean body size (log) projected for the cephalopod group, in the baseline period. Lateral panel represents mean body size predicted for the baseline (blue line) and for future (red line) period. B) Net differences in geometric mean body size predicted between the two periods. In land Cephalopod Global Capture Production per Country [(ton); 2016 data – FAO (2016)].

The predicted range shifts in cephalopods distribution combined with the range contractions projected for most species will result in drastic changes in species composition. Our results point to nestedness being the main driver of cephalopod turnover, with species replacement only predicted to occur in few areas (mainly in the higher latitudes – Fig. 2 left panels). These changes in species composition will result in a less diverse assemblage, as they are projected to occur mainly due to the loss of species, but it's also vital to understand the degree of functional redundancy maintained, to better predict the consequences on ecosystem functioning and resilience (Albouy *et al.*, 2012a). This is particularly important in coastal ecosystems since anthropogenic pressure may act in synergy with climate change intensifying local extinctions (Crain *et al.*, 2009).

The distribution of maximum body size observed in the baseline scenario is consistent with the temperature-size rule (Atkinson, 1994), with larger animals occurring at higher latitudes (and lower temperatures). Rosa *et al.* (2012a) already reported this pattern for the same taxonomic group in the Atlantic Ocean and here we observed it across the globe. According to model projections there is a tendency of slight increase in mean body size towards areas with higher losses in projected richness (Fig. 3), suggesting that these losses are affecting predominantly the smaller species (better represented in tropical latitudes). Which can mean good news for fisheries in these areas, as this tendency might potentially lead to a mitigation of the negative effects of climate change as measured by the total capture (ton). Whereat the higher latitudes the tendency seems to be contrary. Projected changes are more favourable to the countries at higher latitudes, since their fisheries are expected to benefit from the predicted poleward shifts in species richness. Despite projected gain in cephalopod diversity towards the poles, fisheries could need to adjust to the predicted reduction in mean body size.

The effects of ecological change of cephalopod populations driven by overexploitation of fishery resources are still to be fully understood. Yet, one might argue that under the combined effects of intense fishing pressure and climate change, fish are likely to be poor competitors in relation to cephalopods since the latter display faster growth, higher reproductive rates, short life cycles and voracious opportunistic predatory habits (Rodhouse, 2008; Rosa *et al.*, 2013a, b). Cephalopod biomass has not yet replaced fish biomass in the landings, but looking at the continuing growing trend (Doubleday *et al.*, 2016) this hypothesis has to be considered. However, within global climate change context, our results show that there might not be suitable environmental space for cephalopods species to do so. However, our models do not consider the potential for rapid acclimation and adaptation (Munday, 2014), which could give cephalopods time and evolutionary opportunities to adapt to future changes.

Given the increasing number of cross-factorial studies showing the deleterious interacting effects of ocean warming and acidification on the development and physiology of marine invertebrates (Portner, 2008; Findlay *et al.*, 2010; Byrne & Przeslawski, 2013), including cephalopods (Rosa *et al.*, 2014), together with the availability of several new marine variables in the IPCC (2013), pH was included in our models. Which proved to have a great impact in species distribution, as pH was the climatic factor responsible for unsuitable environmental space in 55% of the times, whereas SST was only in 13%. This lead to more pessimistic results, in terms of range contraction due to loss of environmental space, when compare with other studies of these kind (e.g. Cheung *et al.*, 2009; Poloczanska *et al.*, 2013). Also our assumption of limited dispersal and the fact that ecological niche models only take climatic variables into account, when characterizing the habitat suitability, should be taken into considerations when interpreting the results. Furthermore, models predict potential niches not the actual distributions (see Peterson *et al.*, 2011), so it is likely that many areas projected to be occupied in the present and in the future might actually not be. Nevertheless, the first order geographical tendencies of these projections reflect major climatic drivers of change thus being likely to be ecologically meaningful (Garcia *et al.*, 2015).

The global scale and complexity of climate change impacts and the uncertainty in regional climate and earth system projections (Frölicher *et al.*, 2016), calls for improved resolution of regional climate processes. Recent high resolution climate models have allowed to better resolve coastal processes and, in some cases, to reduce regional model biases (Saba *et al.*, 2016), but more need to be done in the terms of data collection and in the integration of biotic processes in more refined models. The use of these data in a "hybrid" mechanistic- empirical approach (as proposed by Robinson *et al.*, 2011) could give us more accurate predictions of what will happen in the ocean of tomorrow.

3.6 References

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3.7 Supplementary material

Table S01 List of the 161 costal cephalopod species used in this study (species marked with * were excluded from the analyses due to few records) with their bathymetric range (min and max depth) and maximum body size (cm).

spID	GroupId	Sp name	Range		BodySize
			min	max	
sp0	L	Afrololigo mercatoris	0	50	640
sp1	L	Alloteuthis africana	20	100	937
sp2	L	Alloteuthis media	0	200	400
sp3	L	Alloteuthis subulata	50	500	50
sp4	L	Ancistroteuthis lichtensteini	0	250	300
sp5	L	Australiteuthis aldrichi	9	61	28
sp6	S	Austrorossia australis	131	665	63
sp7	S	Austrorossia bipapillata	0	240	57
sp8	L	Bathyteuthis abyssicola	100	4200	132
sp9	L	Berryteuthis magister	0	1500	205
sp10	L	Brachioteuthis picta	150	3000	184
sp11	L	Brachioteuthis riisei	50	3000	370
sp12	O	Cistopus indicus	0	50	180
sp13	L	Doryteuthis gahi	0	600	72
sp14	L	Doryteuthis opalescens	0	500	400
sp15	L	Doryteuthis pealeii	0	393	305
sp16	L	Doryteuthis plei	0	370	465
sp17	L	Doryteuthis roperi	50	300	118
sp18	L	Doryteuthis sanpaulensis	0	120	200
sp19	L	Doryteuthis surinamensis*	27	37	380
sp20	O	Eledone cirrosa	0	500	400
sp21	O	Eledone massyae	30	160	75
sp22	O	Eledone moschata	10	300	350
sp23	S	Euprymna berryi	0	107	50
sp24	S	Euprymna morsei	0	200	40
sp25	S	Euprymna tasmanica	0	200	40
sp26	L	Gonatopsis japonicus	0	1000	88
sp27	L	Gonatopsis octopedatus	0	2000	47
sp28	L	Heterololigo bleekeri	0	150	87
sp29	S	Heteroteuthis dispar	0	1588	25
sp30	L	Illex argentinus	80	400	150
sp31	L	Illex coindetii	0	1000	120
sp32	L	Illex illecebrosus	150	510	113
sp33	L	Illex oxygonius	50	550	230
sp34	L	Lepidoteuthis grimaldii	100	2000	120
sp35	L	Loligo forbesii	50	700	39
sp36	L	Loligo reynaudii	0	350	110
sp37	L	Loligo vulgaris	0	500	115
sp38	L	Loliolus affinis	13	15	26
sp39	L	Loliolus beka	0	50	20
sp40	L	Loliolus hardwickei	0	30	200
sp41	L	Loliolus japonica	1	10	394
sp42	L	Loliolus sumatrensis	10	50	422
sp43	L	Loliolus uyii	0	50	200
sp44	L	Lolliguncula argus	0	50	502
sp45	L	Lolliguncula brevis	0	50	270
sp46	L	Lolliguncula diomedeae	0	100	150
sp47	L	Lolliguncula panamensis	0	120	490
sp48	L	Martialia hyadesi	0	200	330
sp49	S	Metasepia pfefferi	3	86	60

sp50	S	Metasepia tullbergi	20	100	70
sp51	S	Neorossia caroli	40	1744	83
sp52	L	Nototodarus gouldi	0	500	160
sp53	L	Nototodarus hawaiiensis	0	650	500
sp54	L	Nototodarus sloanii	0	500	140
sp55	O	Octopus aegina	30	120	100
sp56	O	Octopus burryi	100	200	70
sp57	O	Octopus conispadiceus	100	200	1500
sp58	O	Octopus maya	0	50	1300
sp59	O	Octopus tetricus	0	60	800
sp60	O	Octopus vulgaris	0	200	1200
sp61	L	Onykia carriboea	0	900	72
sp62	L	Onykia robusta	0	900	2300
sp63	L	Pickfordiateuthis bayeri	100	274	75
sp64	L	Pickfordiateuthis pulchella	0	20	22
sp65	L	Pickfordiateuthis vossi	0	150	170
sp66	L	Pyroteuthis margaritifera	75	800	90
sp67	S	Rondeletiola minor	76	496	23
sp68	S	Rossia macrosoma	32	899	85
sp69	S	Rossia pacifica	30	310	90
sp70	O	Scaeurgus unicirrhus	100	800	60
sp71	S	Semirossia equalis	130	260	50
sp72	S	Semirossia tenera	85	135	50
sp73	S	Sepia aculeata	0	60	230
sp74	S	Sepia andreana	0	50	120
sp75	S	Sepia apama	1	100	500
sp76	S	Sepia arabica	80	272	88
sp77	S	Sepia australis	45	345	85
sp78	S	Sepia bandensis	0	200	70
sp79	S	Sepia bertheloti	20	156	175
sp80	S	Sepia braggi	30	86	80
sp81	S	Sepia brevimana	10	100	110
sp82	S	Sepia cultrata	132	800	120
sp83	S	Sepia elegans	0	500	89
sp84	S	Sepia elobyana*	0	NA	53
sp85	S	Sepia esculenta	10	100	180
sp86	S	Sepia grahami	2	84	82
sp87	S	Sepia hedleyi	47	1092	108
sp88	S	Sepia hierredda *	0	50	500
sp89	S	Sepia kobiensis	0	200	90
sp90	S	Sepia latimanus	0	30	500
sp91	S	Sepia longipes	100	300	250
sp92	S	Sepia lorigera	100	300	250
sp93	S	Sepia lycidas	15	100	380
sp94	S	Sepia madokai	20	200	100
sp95	S	Sepia murrayi	0	106	41
sp96	S	Sepia officinalis	0	200	490
sp97	S	Sepia omani	50	210	100
sp98	S	Sepia opipara	83	184	150
sp99	S	Sepia orbignyana	15	570	120
sp100	S	Sepia papuensis	10	155	110
sp101	S	Sepia pharaonis	0	130	420
sp102	S	Sepia plangon	0	83	135
sp103	S	Sepia prabahari	0	100	130
sp104	S	Sepia prashadi	0	200	140
sp105	S	Sepia ramani	0	100	375
sp106	S	Sepia recurvirostra	10	140	170
sp107	S	Sepia rozella	5	183	140
sp108	S	Sepia savignyi	20	50	190

sp109	S	Sepia smith*	33	138	140
sp110	S	Sepia stellifera	0	200	120
sp111	S	Sepia sulcata	150	404	97
sp112	S	Sepia trygonina	20	410	140
sp113	S	Sepia vermiculata	0	290	287
sp114	S	Sepia vietnamica	23	104	70
sp115	S	Sepia vossi	2	140	100
sp116	S	Sepia whitleyana	0	128	174
sp117	S	Sepia zanzibarica	20	125	200
sp118	S	Sepiadarium austrinum	0	200	30
sp119	S	Sepiadarium kochii	0	60	30
sp120	S	Sepiella inermis	0	40	125
sp121	S	Sepiella japonica	0	50	180
sp122	S	Sepiella ornata	20	150	100
sp123	S	Sepiella weberi	0	88	70
sp124	S	Sepietta neglecta	25	475	33
sp125	S	Sepietta obscura	27	376	30
sp126	S	Sepietta oweniana	8	1000	50
sp127	S	Sepiola affinis	15	150	25
sp128	S	Sepiola atlantica	0	200	21
sp129	S	Sepiola birostrata	0	100	22
sp130	S	Sepiola intermedia	8	100	28
sp131	S	Sepiola ligulata	44	380	25
sp132	S	Sepiola parva	0	200	10
sp133	S	Sepiola robusta	26	498	28
sp134	S	Sepiola rondeleti	0	450	60
sp135	S	Sepiola trirostrata	0	200	12,5
sp136	S	Sepiolina nipponensis	0	200	25
sp137	L	Sepioteuthis australis	10	70	70
sp138	L	Sepioteuthis lessoniana	0	100	430
sp139	L	Sepioteuthis sepioidea	0	20	175
sp140	S	Stoloteuthis leucoptera	160	700	18
sp141	L	Todarodes filippovae	0	1200	620
sp142	L	Todarodes pacificus	100	500	1000
sp143	L	Todarodes pusillus	50	500	74
sp144	L	Todarodes sagittatus	0	1000	340
sp145	L	Todaropsis eblanae	20	850	400
sp146	L	Uroteuthis arabica	0	200	379
sp147	L	Uroteuthis bartschi	50	200	350
sp148	L	Uroteuthis bengalensis	0	200	540
sp149	L	Uroteuthis chinensis	15	170	500
sp150	L	Uroteuthis duvaucelii	30	170	400
sp151	L	Uroteuthis edulis	30	200	420
sp152	L	Uroteuthis machelae	54	200	110
sp153	L	Uroteuthis noctiluca	0	50	90
sp154	L	Uroteuthis pickfordi*	0	175	420
sp155	L	Uroteuthis reesi	0	200	248
sp156	L	Uroteuthis robsoni	0	200	240
sp157	L	Uroteuthis sibogae	15	170	290
sp158	L	Uroteuthis singhalensis	30	120	100
sp159	L	Uroteuthis vossi	0	200	136
sp160	L	Watasenia scintillans	100	600	50

Table S02 Table showing the list of models used for each variable analysed. We considered only models that provided the complete series of data from 1860 to 2100 under the historical and RCP 4.5 experiments. The variables analysed included sea surface temperature (CMIP5 variable name 'TOS', in K (converted to ºC in this study)), sea surface salinity ('SOS', in psu), total chlorophyll mass concentration at surface ('Chl', in kg m^{-3}), dissolved oxygen concentration at surface ('O_2', in mol m^{-3}) and pH at surface ('pH', in mol H kg^{-1}).

MODELLING CENTER	COUNTRY	MODEL	Chl	O_2	pH	SOS	TOS
BCC	China	BCC-CSM1-1					x
		BCC-CSM1-1-m					x
CCCma	Canada	CanESM2	x		x	x	x
NCAR	USA	CCSM4				x	x
NSF-DOE-NCAR	USA	CESM1(CAM5)				x	x
CNRM-CERFACS	France	CNRM-CM5	x	x	x	x	x
CSIRO-QCCCE	Australia	CSIRO-Mk3.6.0				x	x
FIO	China	FIO-ESM					x
NOAA GFDL	USA	GFDL-CM3				x	x
NASA GISS	USA	GISS-E2-H				x	x
		GISS-E2-R				x	x
MOHC	UK	HadGEM2-AO				x	x
		HadGEM2-ES	x	x		x	x
IPSL	France	IPSL-CM5A-LR	x	x	x	x	x
MIROC	Japan	MIROC5				x	x
		MIROC-ESM	x		x	x	x
		MIROC-ESM-CHEM	x		x	x	x
MPI-M	Germany	MPI-ESM-LR	x	x	x	x	x
		MPI-ESM-MR	x	x	x	x	x
MRI	Japan	MRI-CGCM3					x
NCC	Norway	NorESM1-M				x	x
TOTAL MODELS			8	5	7	17	21

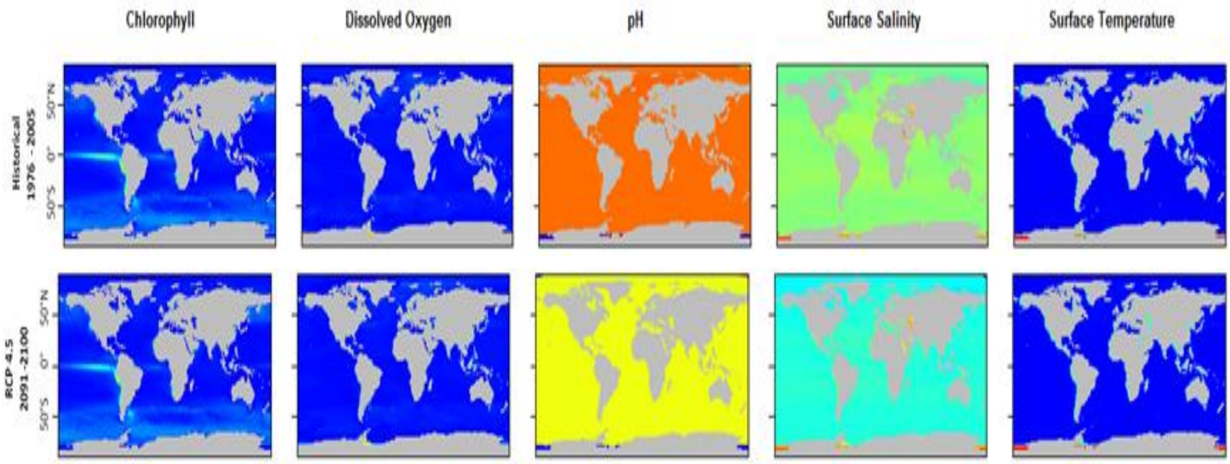

Figure S01 Multi-model mean Standard Deviation across model means per scenario and time period as a measure of precision.

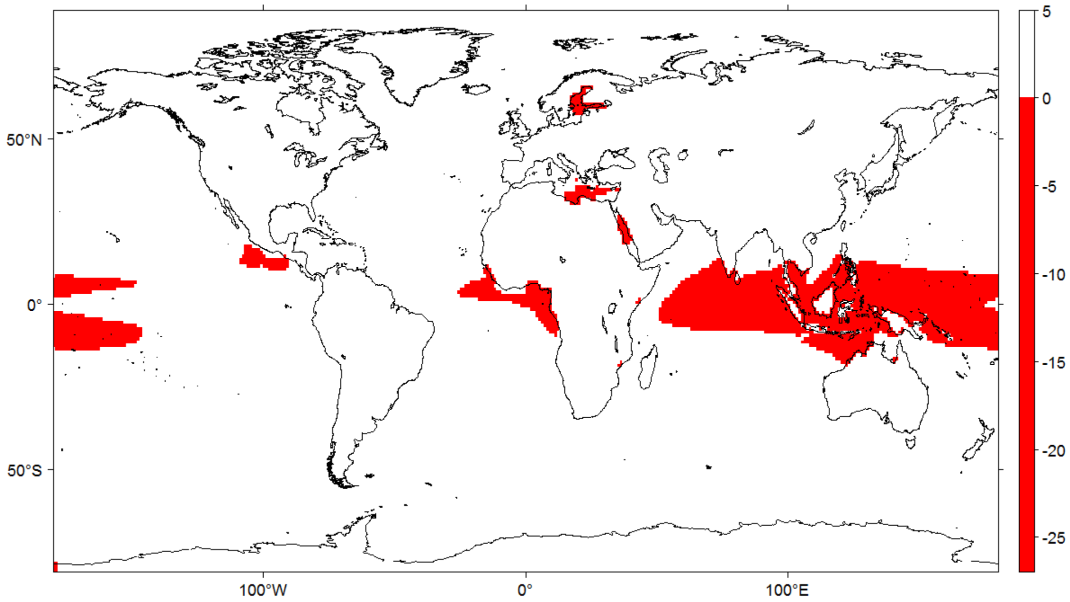

Figure S02 Multivariate Environmental Similarity Surfaces (MESS) analyses for RCP 4.5 scenario. Cells shown in red indicate areas where at least one environmental variable value occurs outside the range of values in the baseline (training) period.

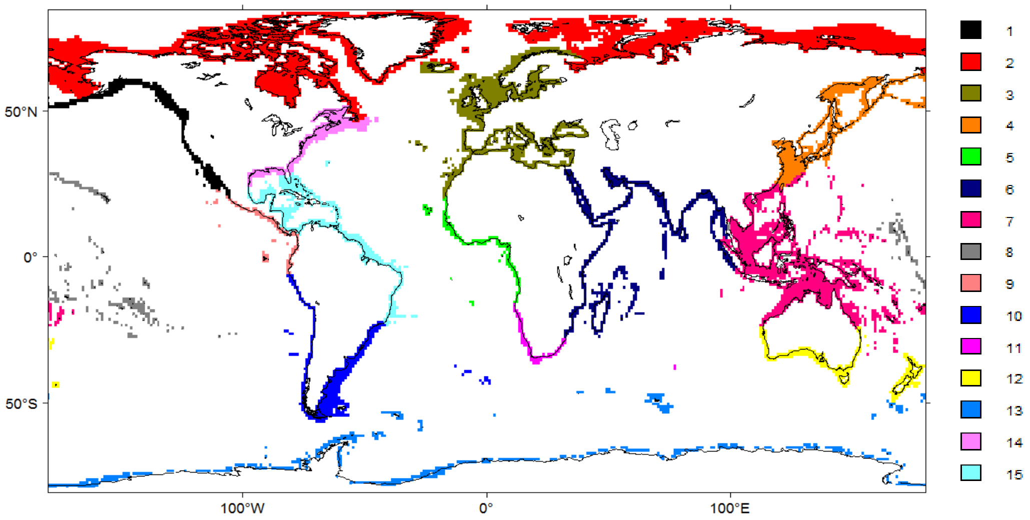

Figure S03 Biogeographic framework. The biogeographic regions used in this work were adapted from the Realms defined by Spalding *et al.* (2007). We created three extra realms to insure the biogeographical division of the Atlantic and Pacific Ocean (extras realms correspond to 1, 14 and 15). Legend: 1-Eastern Temperate Northern Pacific, 2-Artic, 3- Eastern Temperate Northern Atlantic, 4-Western Temperate Northern Pacific, 5-Eastern Tropical Atlantic, 6-Western Indo-Pacific, 7-Central Indo-Pacific, 8-Eastern Indo-Pacific, 9- Tropical Eastern Pacific, 10-Temperate South America, 11-Temperate Southern Africa, 12-Temperate Australasia, 13-Southern Ocean, 14-Western Temperate Northern Atlantic, 15- Western Tropical Atlantic.

CHAPTER 4

4. GLOBAL DIVERSITY AND CATCH VARIATION OF SMALL PELAGIC FISHES IN THE END OF THE 21st CENTURY

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4. GLOBAL DIVERSITY AND CATCH VARIATION OF SMALL PELAGIC FISHES IN THE END OF THE 21st CENTURY

4.1 Abstract

Small pelagic fishes (SPF, anchovies, herrings and sardines) support important fisheries all over the world, but their population dynamics is highly dependent on ocean/climate variability, which raises concern about their viability given ongoing climate change. Here we show that between 45% and 46% of the current habitat of SPF species could lose its suitability, under a range of mitigation scenarios, by the end of the century. In turn, catch potential was projected to decline 32% to 44%, under strong and moderate mitigation scenarios. Between 77-93% of the species were projected to shrink their geographic range and shift their mean latitudes poleward. Anchovies are the biggest losers in a future climate change scenario, with 51% of the species projected to fully lose their habitat suitability. Our results suggest major effects on fisheries worldwide and highlight the need for precautionary management that can easily adapt to projected changes.

4.2 Introduction

Most upwelling regions share a characteristic ‘‘wasp-waist’’ structure, where the bottom (planktonic trophic levels) and top (apex and near-apex levels) of the food chain have high species diversity, while the intermediate trophic level is dominated by one or few small pelagic fish (SPF) species (Bakun *et al.,* 2006). These species exert top-down control on their preys and bottom-up control on their predators and, therefore, dominate the trophic dynamics of these coastal ecosystems (Checkley *et al.,* 2017). SPF support important fisheries all over the world and the economies of many coastal countries are highly dependent on them (Herrick *et al.,* 2009). SPF such as anchovies, herrings and sardines represented about 20% of the total annual world fisheries catch in 2016 (FAO, 2016). Yet, evidence for the widespread effects of climate variability on SPF populations has accumulated over the last decades (Petingas *et al.,* 2012; Chavez *et al.,* 2003) and, though top-down removal of fish biomass can have a strong regulatory effect, their populations appear to be controlled mainly by bottom-up processes (Rosa *et al.,* 2010). Therefore, it is expected that human-induced enhancement of CO_2 concentrations and rise of global mean temperature will dictate profound impacts on SPF distribution and abundance.

4.3 Methods

To estimate these impacts, we used an ensemble of 6 ecological niche models (Diniz-Filho *et al.,* 2009) and 21 earth system models (WCRP, 2010) to project, for the first time, changes in SPF richness, catch potential and geographic range size (comprising 47 anchovies, 33 herrings and 23 sardines species) by the end-century. The two most extreme mitigation scenarios were used to access the range of possible outcomes under alternative scenarios: a strong mitigation (Representative Concentration Pathway, RCP2.6) and the business-as-usual (RCP8.5) scenarios (IPCC, 2013). After fitting the occurrence data to the different modelling techniques implemented in BioEnsembles (Diniz-Filho *et al.,* 2009), we derived a consensus projection for each species potential distribution and calculated SPF richness (Fig. 1), by stacking individual distributional maps on top of each other, for both periods (Peterson *et al.,* 2011). Catch potential was estimated by replacing a 30-year mean capture value for each commercial species (32 species) per FAO area accordingly in the presence/absence matrices (FAO, 2016). We then quantified the potential changes in SPF richness (and catch potential) as the difference between the projected richness (and catch potential) in the future (for both scenarios) and the baseline periods (Fig. 2). Moreover, the projected shifts in latitudinal position and abundance for the major species present in the "Small Pelagic and Climate Change program" (SPACC) regions - California (CC), Humboldt (HC), Benguela (BC) and Kuroshio-Oyashio (KC) Currents, and in the European Atlantic (EA) (Checkley *et al.*, 2012), were also investigated under both future scenarios (for detailed description see Supplementary material).

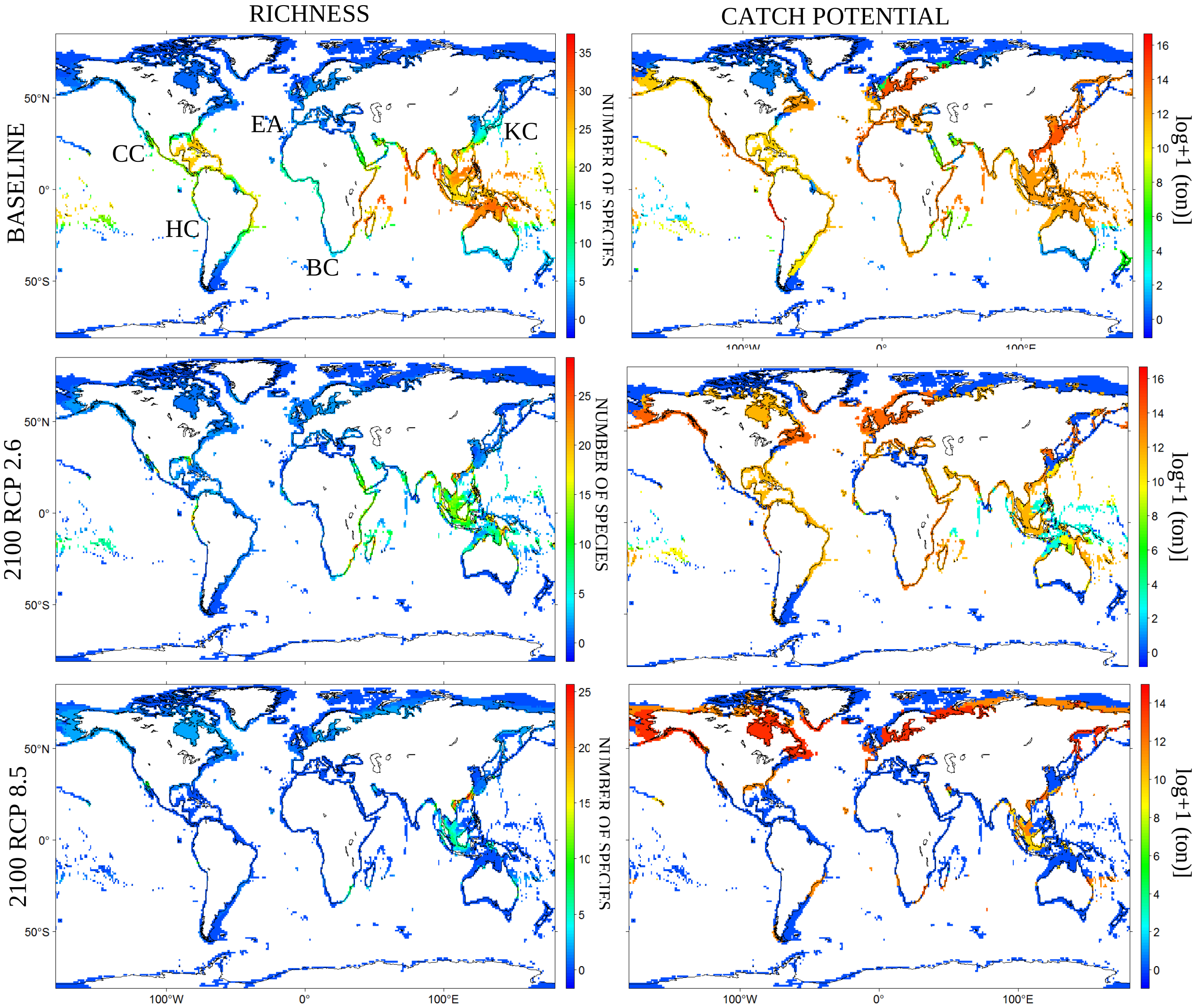

Fig. 1 Projected richness and catch potential for small pelagic fishes for the baseline and end-of-century periods, under the RCP 2.6 and 8.5 scenarios. Acronyms represented in the first map indicate the location of SPACC regions: CC – California Current; HC – Humboldt Current; EA – European Atlantic; BC – Benguela Current; KC – Kuroshio-Oyashio Current.

4.4 Results and Discussion

Our major findings were that global patterns in SPF projected diversity were markedly distinct from the ones projected for catch potential. For the baseline period (Fig. 1; top panels), while total SPF richness was projected to be higher in the Indo-pacific and Caribbean regions, catch potential tended to be higher near the SPACC regions and in the North and Baltic Seas. Among SPF groups, sardines were projected to display higher diversity in the Indo-Pacific area (Fig. S01), whereas anchovies and herrings in the Caribbean region (Fig. S02 and S03, respectively). As for catch potential, herrings were projected to be more abundant at higher latitudes (especially North and Baltic Sea), while anchovies reach their maximum in the HC and KC currents, mostly due to the Peruvian anchoveta (*Engraulis ringens*) and Japonese anchovy (*Engraulis japonicus*) high numbers. Sardines projected catch potential was strongly influenced by the cosmopolitan pilchard *Sardinops sagax* and respective subspecies or lineages (abundant in Australia, CC, BC and KC) and the European pilchard (*Sardina pilchardus*) present in the Northern Atlantic, including Mediterranean Sea (Fig. S01 and S04).

All these patterns changed significantly under the future scenarios, with major losses in richness projected around tropical latitudes, especially under RCP8.5 scenario (Fig. 1, lower panels; Fig. 2). SPF species richness was projected to decline in 44.5% of the total study area (% of cells losing species) in RCP2.6 scenario and 46.2% in the RCP8.5 scenario. These losses were more pronounced in the Indo-Pacific area and Caribbean Sea. As for catch potential, the losses were projected in 32% of total area under RCP2.6 and 44.1% under RCP8.5, especially over the equatorial latitudes and in the Mediterranean and North Seas.

At species-level, almost all species were projected to contract their geographic range in future scenarios, with 8.7% of species projected to completely lose habitat suitability under RCP2.6 (5 herring and 3 anchovy species) and 43.5% in RCP8.5 (23 anchovy, 14 herring and 3 sardine species). On average, SPF were projected to lose up to 77% of range size in RCP2.6 and 93% in RCP8.5 (Fig. 3A). Regarding catch potential this tendency continues, with a mean reduction of 16% in RCP2.6 and 52% in RCP8.5 on projected catch potential (Fig. 3B). Anchovies are the biggest losers in a climate change scenario, with 51% of the species projected to fully lose suitable habitat (Fig. 3A).

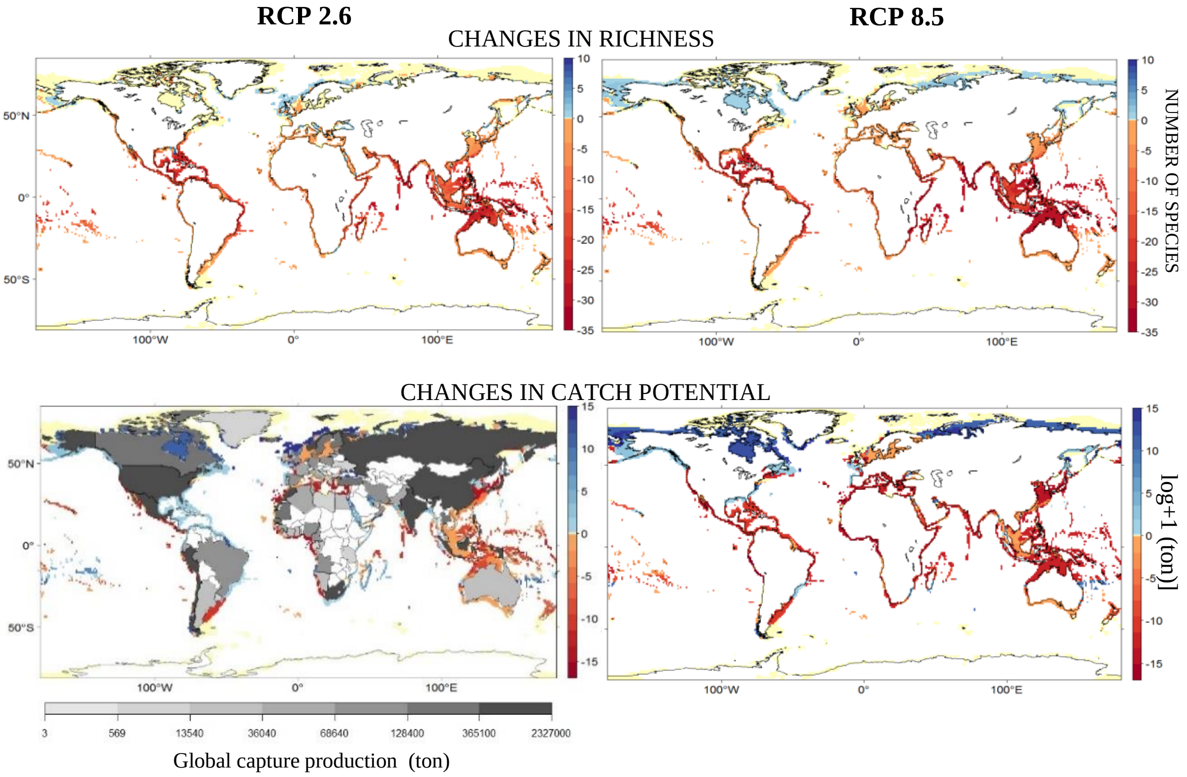

Fig. 2 Projected changes in richness and catch potential (log+1) for small pelagic fishes between the baseline and end-of-century periods, under the RCP 2.6 and 8.5 scenarios. Losses are represented in red and gains in blue. In land shades of grey represent small pelagic fishes* global capture production per country (* defined as the herrings, sardines, anchovies ISSCAAP div/group; 2016 data (ton)).

In the worst case scenario (RCP8.5), pivotal species as the California (*Engraulis mordax*) or Japonese (*Engraulis japonicus)* anchovy and the Peruvian anchoveta [*Engraulis ringens*; world's largest single-species fishery (FAO, 2016)] are projected to completely lose their suitable habitat (Fig. 4). Although such drastic projections call for cautious interpretation, as they may be linked to their current narrow geographic distribution, that leads to a confine projected environmental niche, which can result in an under estimation of suitable habitat available to these species. The few exceptions to this downward trend were the Atlantic and the Pacific herring projected to expand their geographic range and increase catch potential, under both scenarios (Fig. 4). Such trend is linked with the projected poleward shift of suitable habitat and can add value to the North European fisheries, as this industry is heavily dependent on this resource [Atlantic herring is the top 3 in world captures (FAO, 2016)].

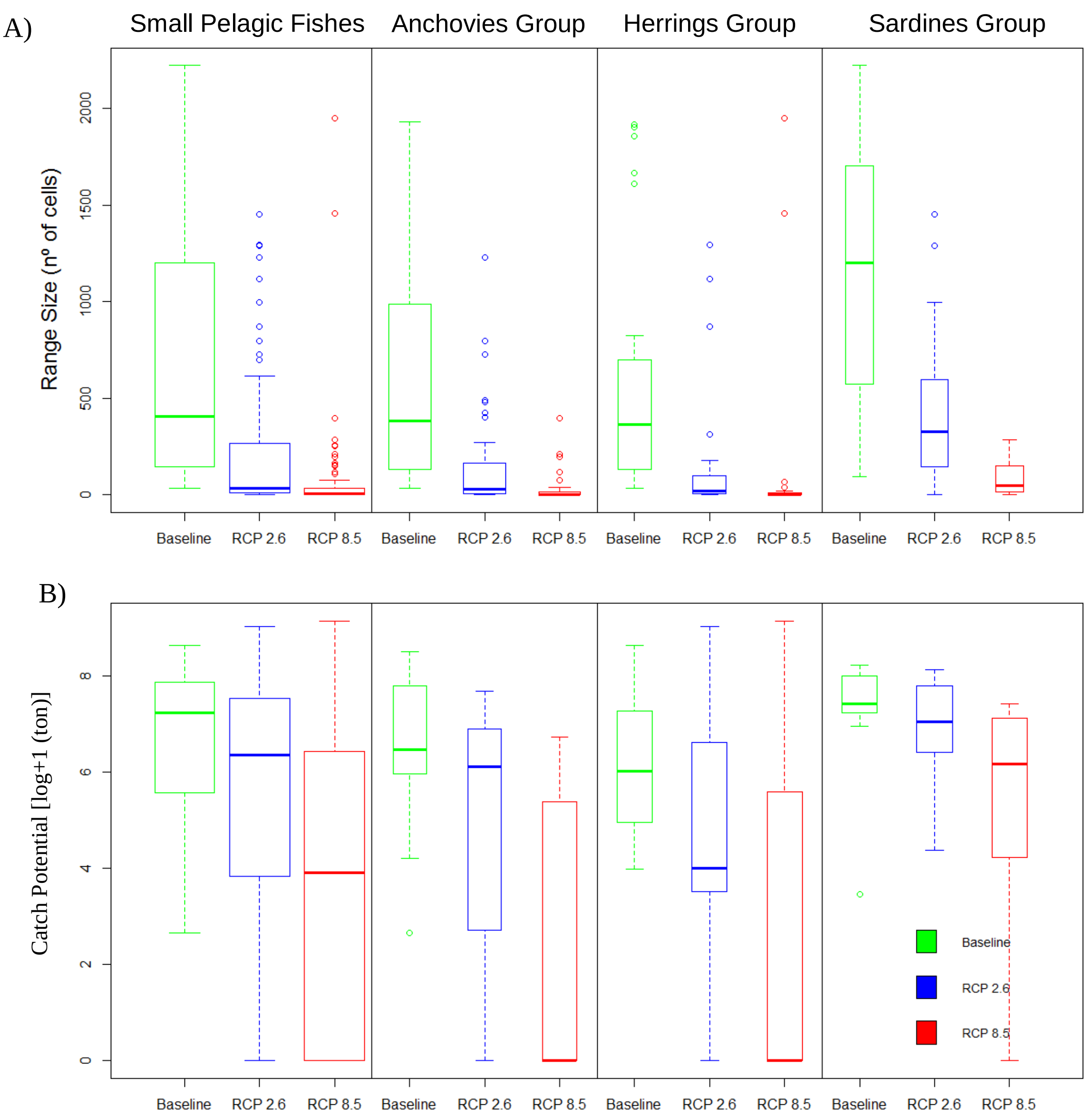

Fig. 3 A) Projected geographic range size variation (measured as the number of cells where the species is present) for small pelagic fishes (as sum of all species) and decomposed in the major groups (anchovies, herrings and sardines) for the baseline (green) and end-of-century periods, under the RCP 2.6 (blue) and 8.5 (red) scenarios. B) Variation in projected catch potential (log) for small pelagic fishes and decomposed in the major groups (anchovies, herrings and sardines) for the baseline (green) and end-of-century periods, under the RCP 2.6 (blue) and 8.5 (red) scenarios.

Overall our models project a significant reduction in the number of SPF species present by end- century. And a significant shift in the catch potential patterns in northern latitudes (higher than 50ºN; Fig. 2). Also we found significant relations between projected changes in richness and the Gross Domestic Product (GDP) per person of the countries analysed (N=88 countries; p<0.005), with a tendency of higher losses occurring in countries with lower income (see Supplementary Figure S05). We anticipate this could have serious consequences for fisheries worldwide, especially in developing countries (Southeast Asia particularly), where the increasing demand for human consumption and mariculture have already reduced SPF resources to a precarious state (Herrick *et al.,* 2009).

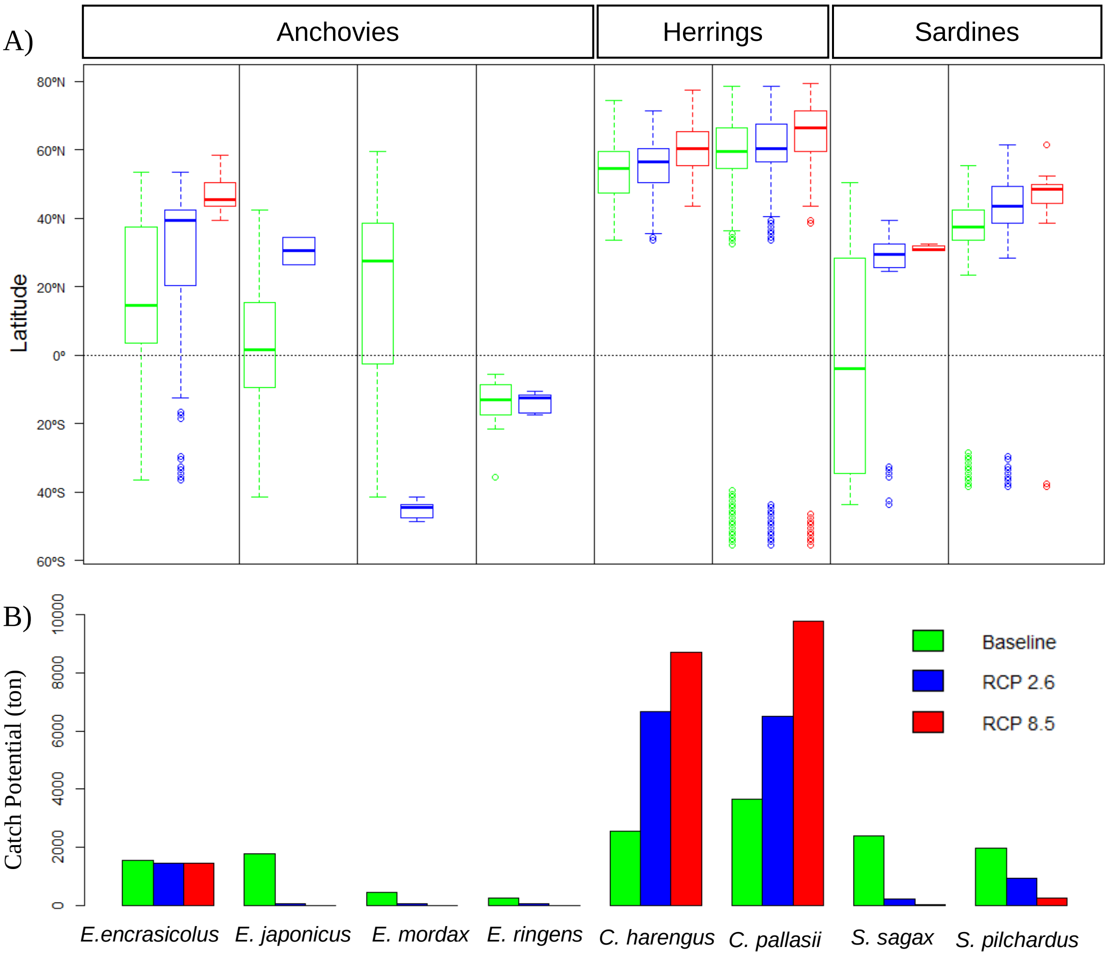

Fig. 4 A) Latitudinal shifts projected for the major SPF species (ANCHOVIES: *Engraulis encrasicolus*, *Engraulis japonicus*, *Engraulis mordax, Engraulis ringens;* HERRINGS: *Clupea harengus, Clupea pallasii;* SARDINES: *Sardinops sagax*, *Sardina pilchardus*), in the baseline (green) and end-of-century periods, under the RCP 2.6 (blue) and 8.5 (red) scenarios. B) Variation in projected catch potential (ton) for the major SPF species, in the baseline (green) and end-of-century periods, under RCP8.5 and RCP2.6.

Poleward shifts to higher latitudes have already been observed for some SPF species (McLeod *et al.,* 2012; Barange *et al.,* 2009) and were projected to increase in future scenarios for several other marine taxa (e.g. Jones & Cheung, Barton *et al.,* 2016;

Barange *et al.,* 2018). As our results demonstrate, SPF may be particularly affected with the resulting assemblages being much less diverse and with narrower ranges of suitable habitat left to occupy. In addition, climate change will increase stress on the physiology of these resources, making the populations less resilient to unfavourable environmental conditions (Faleiro *et al.,* 2016) and more vulnerable to excessive exploitation.

Model assumptions and limitations call for careful interpretation of the projected responses to climate change (Chueng *et al.,* 2016). First, the presented results are based on potential changes in habitat suitability, which relate to the realized niche of the species that may or may not be fully occupied (Peterson *et al.,* 2012). Second, the coarse resolution of the CMIP5 climate models limits the ability to predict finer processes affecting species distribution, such as stratification or variation in coastal currents that can significantly impact larval dispersal patterns and other processes (Brochier *et al.,* 2013)**.** Recent high-resolution climate projections (Saba *et al.,* 2016) show a bias in global climate model simulations, indicating greater warming than projected by coarse resolution climate projections in some areas. Third, our model does not consider the potential for rapid acclimation and adaptation (Munday *et al.,* 2014), which could give SPF time and evolutionary opportunities to adapt to future changes. Despite these reservations, we believe our results highlight the sensibility of different SPF species and geographical areas to climate change and point out where regional studies at a finer scale resolution are needed to inform management and political measures.

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4.6 Supplementary material

4.6.1 Online Methods

Species data

Small pelagic fishes species (SPF) used in this study were chosen based on several criteria: Clupeoidei suborder, strictly marine, maximum length of 50 cm and finally we restricted our analysis to sardines, anchovies or herrings. Witch left us with 113 species of SPF (see list in Supplemental Table S01).

Occurrence locality records for selected species were downloaded from the Ocean Biogeographic Information System (OBIS) database via the Global Biodiversity Information Facility (GBIF) biodiversity information portal (http://www.gbif.org); data were quality controlled by removing duplicate records, data points which did not fall within the area covered by our environmental layers (e.g. terrestrial records) and records falling outside the bathymetric range of the species. The bathymetry of the ocean was obtained from ETOPO2 (ETOPO2, 2010) and resampled to a 1º x 1º latitude/longitude grid. The remaining records for each species were then compare against the range map for that species and records were removed, if outside the range map, using ArcGIS 9.3 (ESRI, 2006).Information on geographic range, habitat and biology of SPF were compiled based on FishBase (http://www.fishbase.org/search.php), *International Union for Conservation of Nature* (IUCN) Red List of Threatened Species ™ (http://www.iucnredlist.org/#) and Food and Agriculture Organization of the United Nations (FAO) Species Catalogue VOL.7 – Clupeoid Fishes of the world (Whitehead, 1985; Whitehead *et al.,* 1988).

To avoid statistical bias in ecological niche modelling (ENM) fitting, 21 species (market with * in Table S1) were excluded from the analyses – corresponding to those with fewer than 20 records over the study area (Wisz *et al.,* 2008).

Climatic data

We used 30-year averages of five climate variables (sea surface temperature, sea surface salinity, total chlorophyll mass concentration at surface, dissolved oxygen concentration at surface and ocean surface pH) from Earth System Models (ESM) developed for CMIP5. There were 21 ESM's from 15 climate centres in 9 countries that modelled at least one of the variables analysed (Table S01). For each model and variable, we used the period 1976–2005 from the historical experiment, to establish the baseline period. And the period 2071–2100, to define our future scenarios. The two most extreme mitigation scenarios were used to access the range of possible outcomes under alternative scenarios: a rapid CO_2 mitigation (Representative Concentration Pathway, RCP2.6) and the business-as-usual (RCP8.5) scenarios (IPCC, 2013), with CO_2 concentrations increase projected to vary between 421 and 936 ppm by 2100, respectively (Vuuren *et al.,* 2011).

Climate data were publicly available from the World Climate Research Programme (http://cmip-pcmdi.llnl.gov/cmip5/availability.html). Sea surface temperature and surface seawater salinity have monthly frequency while the other three variables have annual data. We only extracted the first layer (*i.e.* surface) for chlorophyll, dissolved oxygen, and pH. All parameters were interpolated into a common 1° by 1° grid prior to calculating multi-model means (Mora *et al.,* 2013). We estimated multi-model variability by calculating the standard deviation of model means among Earth System Models per variable and time period (Figure S06). There are several methods to ensemble ESM's, but average of several coupled climate models is usually found to agree better with observations than any single model (Tebaldi & Knutti, 2007).

To match the resolutions of species and climate data, all datasets were re-sampled in ArcGIS9.3 (ESRI, 2006) to the 1° grid used for species. Data processing and statistical analyses were performed using R software (R, 2011).

Ecological Niche Models

In order to constrain algorithmic uncertainty associated with Ecological Niche Models (ENM's) we implemented an ensemble forecasting method (Araújo & New 2007). Models were fitted using six different statistical techniques implemented in BioEnsembles (Diniz-Filho *et al.,* 2009): (1) BIOCLIM, (2) Euclidean distance (EUC), (3) Generalized Linear Models (GLM), (4) Generalized Additive Models (GAM), (5) Multivariate Adaptive Regression Splines (MARS), (6) Maximum Entropy (Maxent).

For each species, data were randomly partitioned into calibration (75%) and validation (25%) dataset, the procedure was repeated 5 times, maintaining the observed prevalence of species in each partition, and models for each species were fit and evaluated using the True Skill Statistic (TSS) (Allouche *et al.,* 2006). Only the models that performed above 'good' levels (TSS values > 0.7) were included in the final ensemble (Thuillier *et al.,* 2019). Weighted median consensus forecasts were computed (Albouy *et al.,* 2012) and used to build final projections, using 100% of the data, as data partitions have been shown to add significant uncertainty to forecasts (Araújo *et al.,* 2009) (TSS for final ensemble performed at 'excellent' levels = 0.89±0.078).

Using projected future climatic conditions we estimated changes in the geographic location of environmental niches for each species. We have restricted our analyses to the continental shelf (200 m depth limit) as small pelagic species are known to be strongly associated with coastal upwelling regions (Checkley et al., 2009). Also, we trimmed the projected climatic suitability for both periods, so a species was only allowed to move to an adjacent realm (fig. S06 shows the realms used in this study – adapted from Spalding *et al.,* 2007). Even though several factors can contribute to a species not fulling occupying its potential niche (Colwell & Rangel, 2009), we considered unrealistic that a SPF (or SPF larvae) could move beyond important geographical barriers and disperse across major oceans (reason we added extra realms to Spalding *et al. (2007)* classification, dividing Atlantic and Pacific Ocean in Western and Eastern).

Projected changes in richness and abundance of small pelagic fishes

We determined each species potential distribution and calculated SPF richness (Fig. 1), by stacking individual distributional maps on top of each other, for both periods (Peterson *et al.,* 2011). We then quantified the potential changes in SPF richness as the difference between the projected diversity in the future (for both scenarios) and the baseline periods (Fig. 2). To infer how SPF abundance might be affected by climate change we collected the global capture production [1985 - 2016 averaged data (FAO, 2016)] for all commercial species available [32 species market as # in table S01 (defined as the herrings (11), sardines (11), anchovies (10) ISSCAAP div/group and identified at species level)] by

FAO area and replaced accordingly in the 1° grid presence/absence matrix (all pixels inside a FAO area assume the 30 –year mean capture production for that area for each species). For future scenarios the mean capture production value of all FAO areas occupied by the species was used, as we don´t want to restrict species movement or have sufficient information on the fisheries trends. We then determined SPF overall catch potential through time (in tons), as a proxy for abundance (since catch data can be heavily influenced by fisheries regulations and market drivers), (Fig. 1) and quantified potential changes as mentioned for diversity (Fig. 2). Logarithmic transformation (log+1) was used in order to remove the effects of really high catch data and account for non-normal distribution and applied the geometric rather than the arithmetic mean (Fisher *et al.*, 2010). Since global capture production are derived from landing statistics it's expected a bias towards countries with higher effort in SPF fisheries, nevertheless is relevant to have a picture of how catch potential of this group looks at a global scale and how climate change might be projected to alter it. Global capture production per country for SPF [defined as the herrings, sardines, anchovies ISSCAAP div/group; FAO (2016)] was used as a proxy for countries dependency on resource (Fig. 2 – In land shades of grey). The same analyse was performed for the groups used in this study (sardines, anchovies and herrings) at an individual scale (Fig. S03-S05).

Variation in range size and abundance

To quantify the potential effect of climate change on species range sizes we calculate the relative loss or gain of the potential geographic ranges sizes (measured as number of cells occupied by a species) between the baseline and future period, for SPF (as a sum of all species analysed) and for the major groups (sardines, anchovies and herrings; Fig. 3A). The same analyse was made for catch potential (Fig. 3B). We assessed the differences in mean range size through time using a Mann–Whitney-Wilcoxon Test for paired samples.

Latitudinal shifts

To predict the latitudinal shifts that major SPF species might undergo due to climate change, we analysed the principal sardines, anchovies and herrings species present in the Small Pelagic and Climate Change program (SPACC) regions[21], namely California (CC), Humboldt (HC), Benguela (BC) and Kuroshio-Oyashio (KC) Currents, and in the European

Atlantic (EA). This was made by analysing the shift in mean latitude for each species and period (Fig. 4A).

Regression

To assess the relation between projected changes in richness and catch potential per country and relevant socio-economic metrics, a regression analyses was made with different metrics (total SPF capture production (ton), Gross Domestic Product/person ($USD), population size (number of individuals) and fish consumption/person (g of protein)) and present the results of the significant relations (Fig. S05; socio-economic data from http://data.worldbank.org/).

MESS analyse

To determine the extent of environmental differences between baseline and future climates a Multivariate Environmental Similarity Surfaces (MESS) analyse was performed (Elith & Philips, 2010). For each cell, the degree of similarity between the new environments and those in the baseline period was computed (negative values represent dissimilarity), as models are less reliable when predicting outside their domain (Barbosa *et al.,* 2009). These calculations were performed using the modEvA R package (Barbosa *et al.,* 2016). Results are presented in fig. S08 and present in red the areas with higher uncertainty.

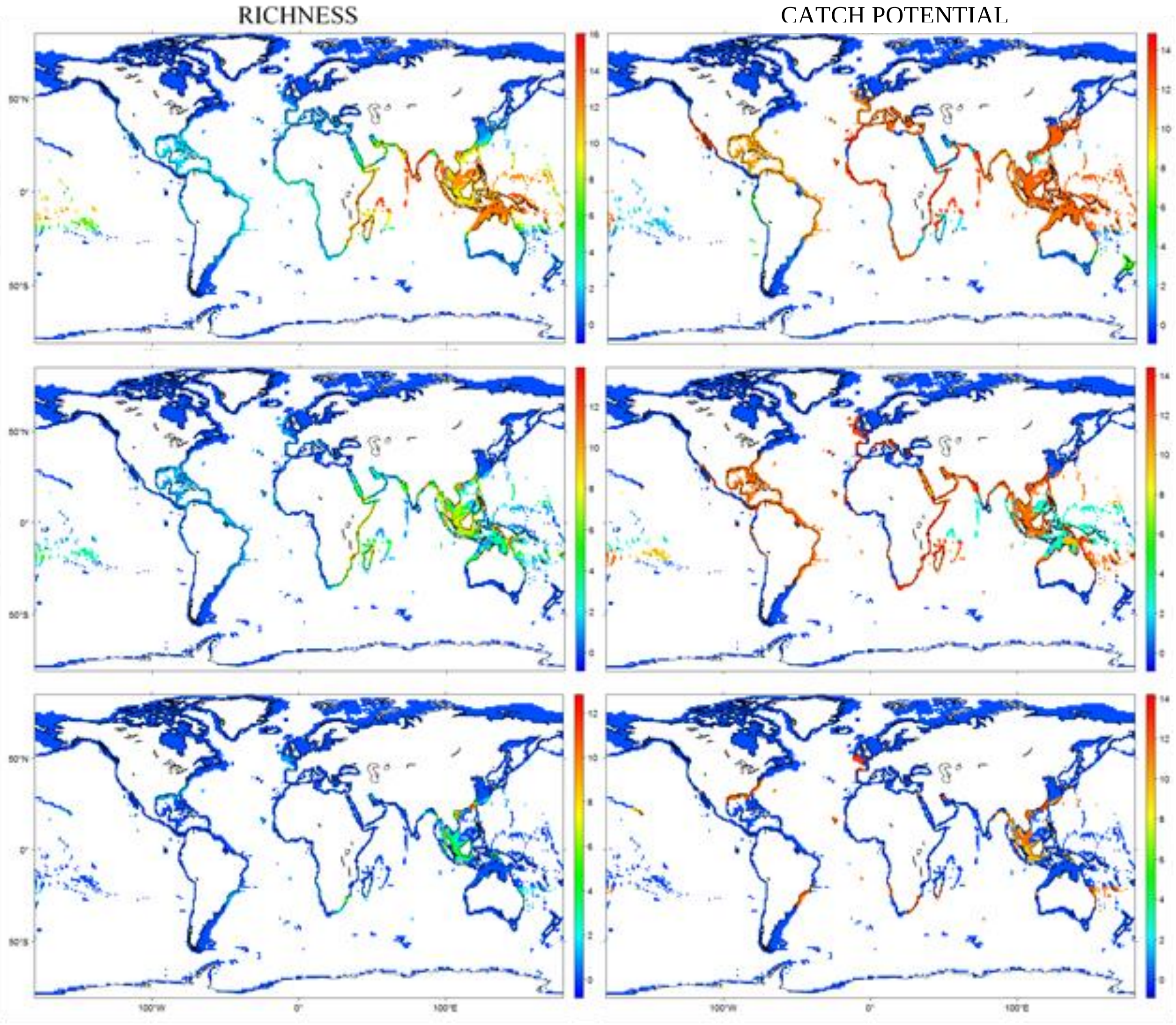

Fig. S01 Projected richness and catch potential for sardine species for the baseline and end-of-century periods, under the IPCC AR5 RCP 2.6 and 8.5 scenarios.

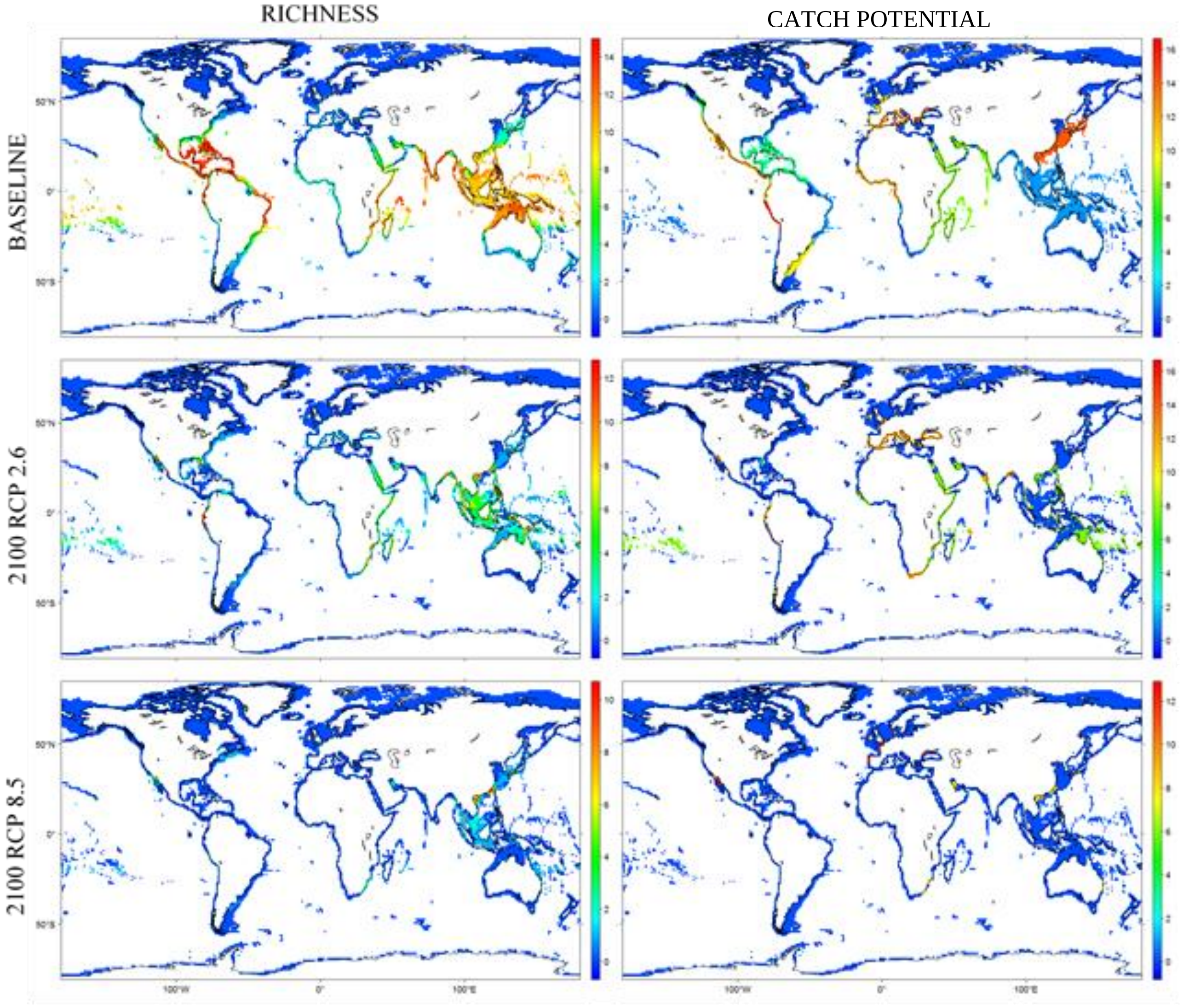

Fig. S02 Projected richness and catch potential for anchovy species for the baseline and end-of-century periods, under the IPCC AR5 RCP 2.6 and 8.5 scenarios.

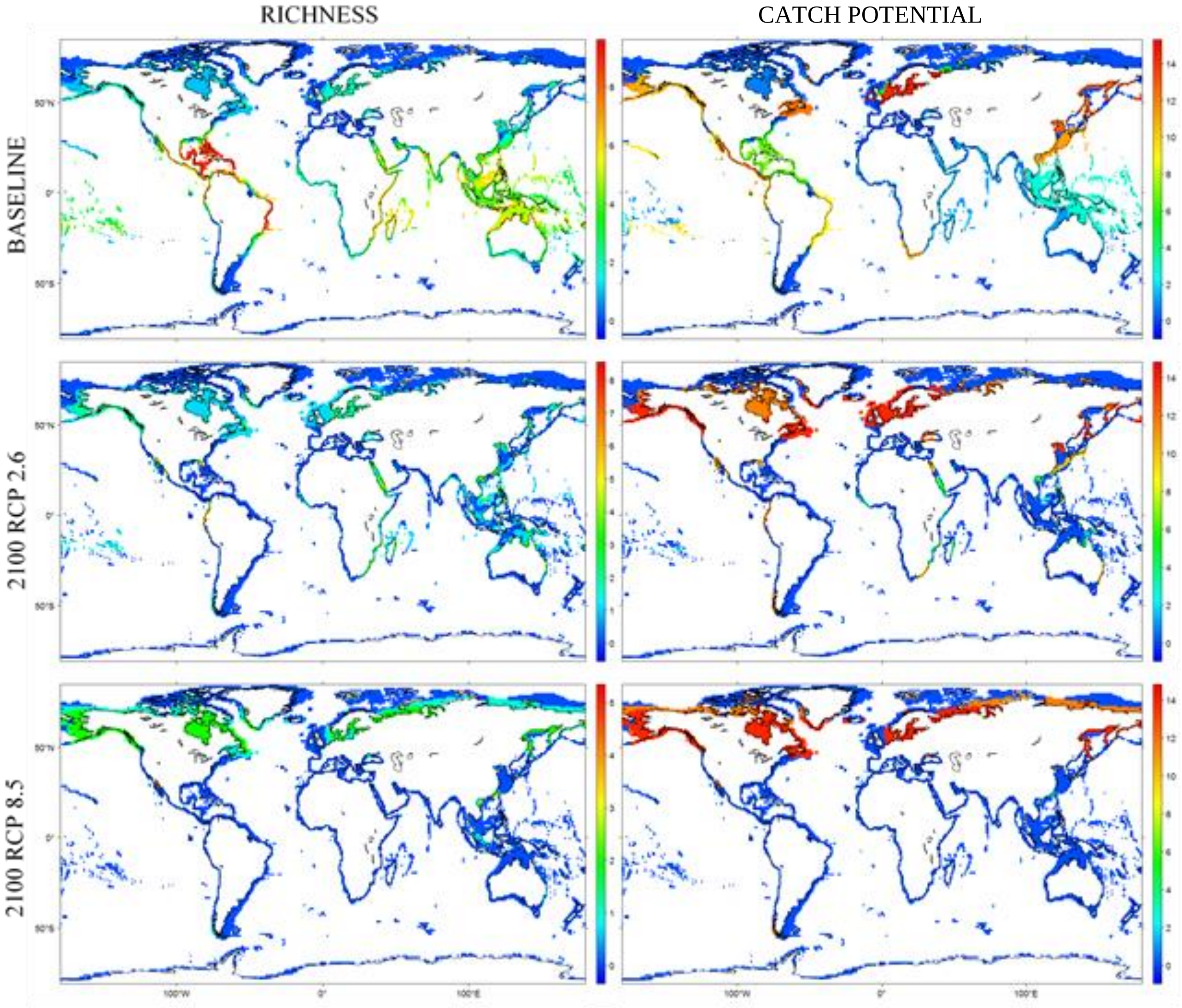

Fig. S03 Projected diversity and abundance for herring species for the baseline and end-of-century periods, under the IPCC AR5 RCP 2.6 and 8.5 scenarios.

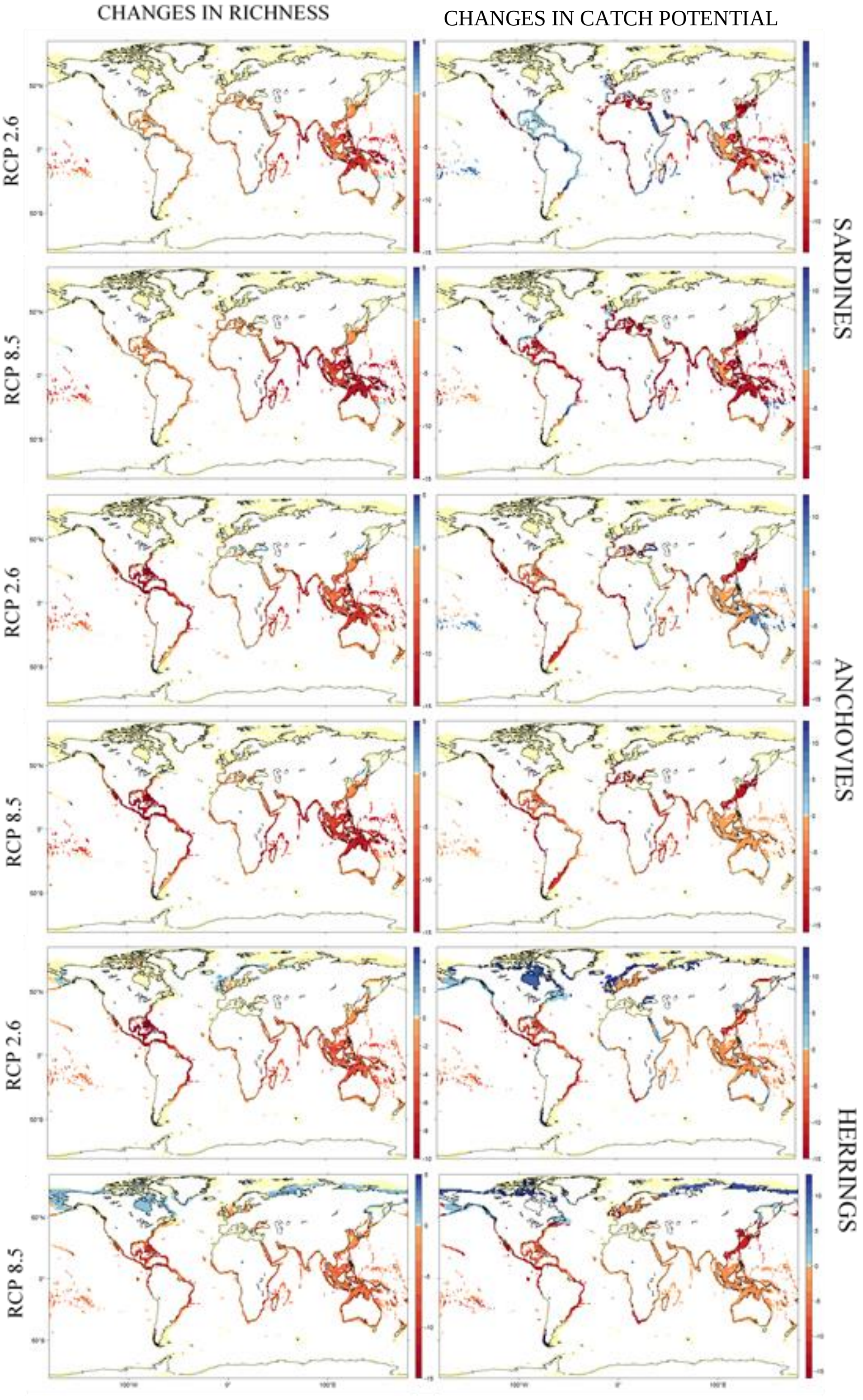

Fig. S04 Projected changes in richness and catch potential for small pelagic major groups (sardines, anchovies and herrings) between the baseline and end-of-century periods, under the IPCC AR5 RCP 2.6 and 8.5 scenarios.

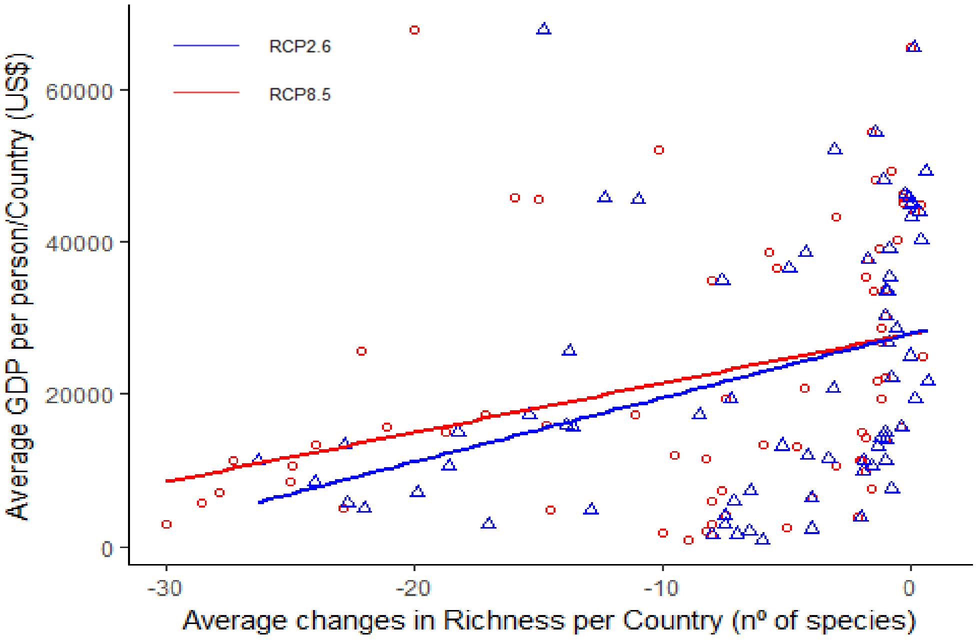

Fig. S05 Relation between average changes in richness and Gross Domestic Product (GDP) per person for the countries with continental shelf (N=88 countries). The trend line for RCP2.6 is modelled with $\gamma=844\chi+28002$ ($r^2=0.35$, $P<0.005$) and trend line for RCP8.5 with $y=649x+27963$ ($r^2=0.35$, $P<0.005$).

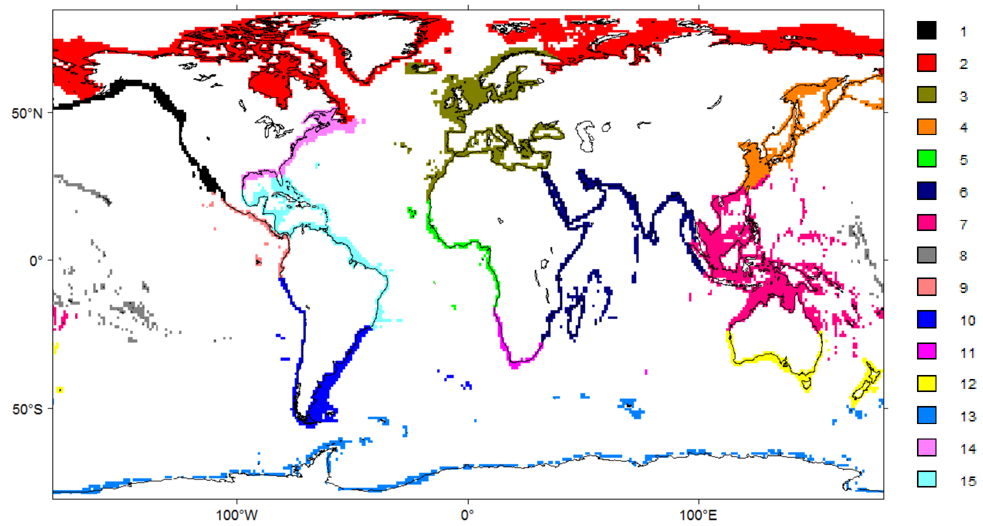

Fig. S06 Biogeographic regions used in this work [adapted from the realms proposed by Spalding *et al*. (2007)]. Three extra realms were included to insure the biogeographical division of the Atlantic and Pacific Ocean (extras realms correspond to 1, 14 and 15). Legend: 1-Eastern Temperate Northern Pacific, 2-Artic, 3- Eastern Temperate Northern Atlantic, 4-Western Temperate Northern Pacific, 5-Eastern Tropical Atlantic, 6-Western Indo-Pacific, 7-Central Indo-Pacific, 8-Eastern Indo-Pacific, 9- Tropical Eastern Pacific, 10-Temperate South America, 11-Temperate Southern Africa, 12-Temperate Australasia, 13-Southern Ocean, 14-Western Temperate Northern Atlantic, 15- Western Tropical Atlantic.

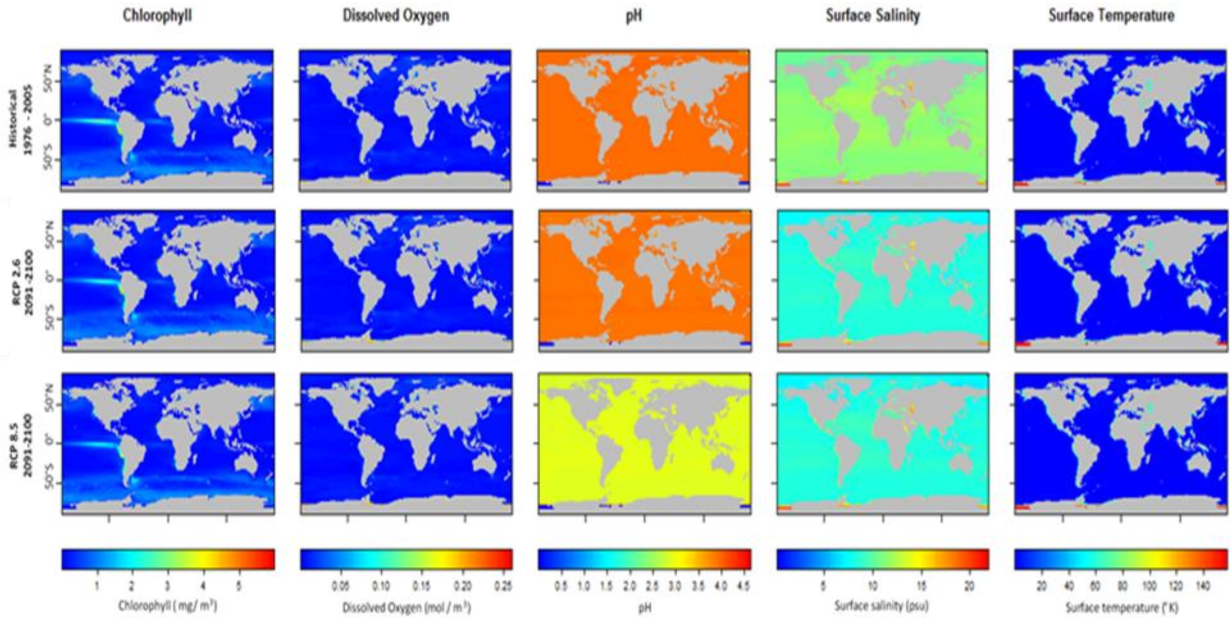

Fig. S07 Standard deviation across climatic model means per scenario and time period as a measure of variability in the multi-model ensemble of Earth System Models (ESM) used.

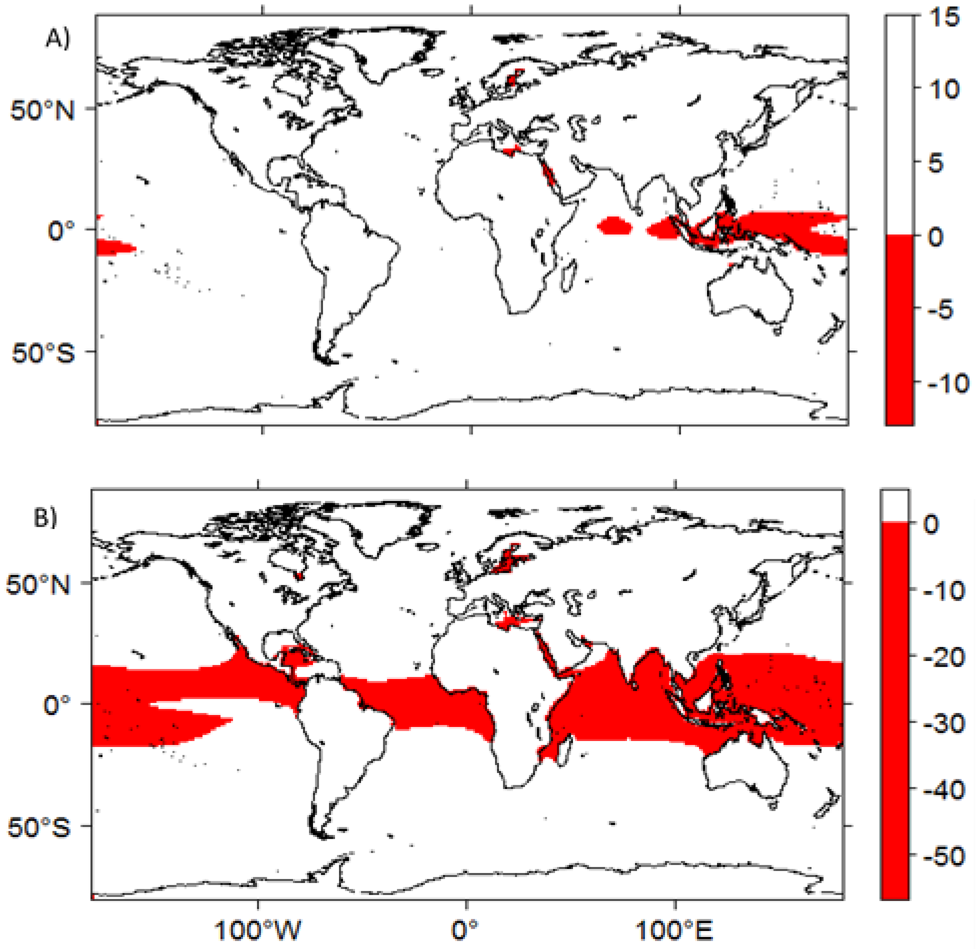

Fig. S08 Multivariate Environmental Similarity Surfaces (MESS) analyses for A) RCP 2.6 and B) RCP 8.5 scenarios. Cells shown in red indicate areas where at least one environmental variable value occurs outside the range of values in the baseline (training) period.

Table S01 List of species used for this study, the bathymetric range occupied by each species (Min and Max Depth in meters (m)), their standard body size (Bsize) in cm and the group they belong to. Species marked with (*) were excluded from the analysis due to few records and the species marked with (#) represent the ones with economic value and were included in the abundance analysis.

id	Species	Min	Max	Bsize	Group
sp_1	Amblygaster_clupeoides	0	50	17	sardine
sp_2	Amblygaster_leiogaster	0	50	23	sardine
sp_3	Amblygaster_sirm#	10	75	24	sardine
sp_4	Anchoa_analis*	1	2	10	anchovy
sp_5	Anchoa_argentivittata	0	50	12.5	anchovy
sp_6	Anchoa_cayorum*	0	10	11	anchovy
sp_7	Anchoa_chamensis*	0	50	6	anchovy
sp_8	Anchoa_colonensis	0	50	14	anchovy
sp_9	Anchoa_compressa	0	50	13.3	anchovy
sp_10	Anchoa_cubana	0	60	10	anchovy
sp_11	Anchoa_curta	0	50	8.9	anchovy
sp_12	Anchoa_delicatissima*	0	50	12	anchovy
sp_13	Anchoa_eigenmannia	0	50	8	anchovy
sp_14	Anchoa_exigua	0	50	7.5	anchovy
sp_15	Anchoa_helleri	0	50	8.5	anchovy
sp_16	Anchoa_hepsetus#	1	70	15.3	anchovy
sp_17	Anchoa_ischana	0	50	14	anchovy
sp_18	Anchoa_lamprotaenia	0	50	12	anchovy
sp_19	Anchoa_lucida	1	60	13.2	anchovy
sp_20	Anchoa_lyolepis	1	54	12	anchovy
sp_21	Anchoa_mitchilli	0	70	10	anchovy
sp_22	Anchoa_nasus#	0	142	17	anchovy
sp_23	Anchoa_parva	0	50	6	anchovy
sp_24	Anchoa_pectoralis*	1	22	6.8	anchovy
sp_25	Anchoa_spinifer	1	55	24	anchovy
sp_26	Anchoa_starksi	0	50	7.7	anchovy
sp_27	Anchoa_tricolor*	0	50	11.8	anchovy
sp_28	Anchoa_walkeri	0	50	14.5	anchovy
sp_29	Anchovia_clupeoides	0	50	30	anchovy
sp_30	Anchovia_macrolepidota	0	50	25	anchovy
sp_31	Anchoviella_brevirostris	1	50	9	anchovy
sp_32	Anchoviella_lepidentostole	1	50	11.6	anchovy
sp_33	Anchoviella_perfasciata	0	50	11	anchovy
sp_34	Cetengraulis_endutulus#	10	475	15	anchovy
sp_35	Cetengraulis_mysticetus#	0	32	22	anchovy
sp_36	Chirocentrodon_bleekerianus	20	60	11	herring
sp_37	Clupea_harengus#	0	364	45	herring
sp_38	Clupea_pallasii#	0	475	46	herring
sp_39	Dussumieria_acuta#	10	20	20	sardine
sp_40	Dussumieria_elopsoides#	0	50	20	sardine
sp_41	Encrasicholina_devisi	10	13	8	anchovy
sp_42	Encrasicholina_heteroloba	20	50	12	anchovy
sp_43	Encrasicholina_punctifer#	5	35	13	anchovy
sp_44	Encrasicholina_purpurea*	0	50	7.5	anchovy
sp_45	Engraulis_anchoita#	30	200	17	anchovy
sp_46	Engraulis_australis	31	70	15	anchovy
sp_47	Engraulis_capensis*	0	450	17	anchovy
sp_48	Engraulis_encrasicolus#	0	400	20	anchovy
sp_49	Engraulis_eurystole	124	282	15.5	anchovy
sp_50	Engraulis_japonicus#	0	400	18	anchovy
sp_51	Engraulis_mordax#	0	219	24.8	anchovy
sp_52	Engraulis_ringens#	3	80	20	anchovy

sp_53	Etrumeus_teres#	0	125	33	herring
sp_54	Etrumeus_whiteheadi#	0	200	22	herring
sp_55	Harengula_clupeola#	0	50	15	herring
sp_56	Harengula_humeralis#	0	50	17.2	herring
sp_57	Harengula_jaguana#	0	22	15	herring
sp_58	Harengula_thrissina	0	50	8	herring
sp_59	Herklotsichthys_blackburni*	0	50	10.5	herring
sp_60	Herklotsichthys_castelnaui	0	50	14	herring
sp_61	Herklotsichthys_dispilonotus	0	50	8.5	herring
sp_62	Herklotsichthys_gotoi*	0	50	9	herring
sp_63	Herklotsichthys_koningsbergeri	0	50	13	herring
sp_64	Herklotsichthys_lippa	0	475	16	herring
sp_65	Herklotsichthys_lossei*	0	50	8	herring
sp_66	Herklotsichthys_punctatus	0	50	8.5	herring
sp_67	Herklotsichthys_quadrimaculatus#	1	13	14	herring
sp_68	Herklotsichthys_spilurus	0	50	8.5	herring
sp_69	Jenkinsia_kamprotaenia	0	50	7.5	herring
sp_70	Jenkinsia_majua	0	50	5.5	herring
sp_71	Jenkinsia_stolifera	0	50	4	herring
sp_72	Lile_stolifera	0	50	13	herring
sp_73	Opisthonema_berlangai*	0	50	26	herring
sp_74	Opisthonema_bulleri	0	50	19.6	herring
sp_75	Opisthonema_libertate#	0	100	25	herring
sp_76	Opisthonema_medirastre	0	50	22	herring
sp_77	Opisthonema_oglinum#	0	50	25	herring
sp_78	Pliosteostoma_lutipinnis	0	50	25	herring
sp_79	Sardina_pilchardus#	10	100	25	sardine
sp_80	Sardinella_albella	0	50	14	sardine
sp_81	Sardinella_aurita#	0	350	30	sardine
sp_82	Sardinella_brachysoma	0	50	13	sardine
sp_83	Sardinella_brasiliensis#	5	475	25	sardine
sp_84	Sardinella_frimbriata	0	50	13	sardine
sp_85	Sardinella_gibbosa#	10	70	17	sardine
sp_86	Sardinella_hualiensis*	0	50	12.5	sardine
sp_87	Sardinella_lemuru#	15	100	23	sardine
sp_88	Sardinella_longiceps#	20	200	23	sardine
sp_89	Sardinella_maderensis#	0	80	37.3	sardine
sp_90	Sardinella_marquesensis*	0	50	16	sardine
sp_91	Sardinella_melanura	0	50	15.2	sardine
sp_92	Sardinella_richardsoni*	0	50	12	sardine
sp_93	Sardinella_rouxi	0	50	16	sardine
sp_94	Sardinella_sindensis	0	50	17	sardine
sp_95	Sardinella_zunasi*	5	475	18	sardine
sp_96	Sardinops_sagax#	0	200	36	sardine
sp_97	Spratelloides_delicatulus	0	50	7	herring
sp_98	Spratelloides_gracillis#	10	475	10.5	herring
sp_99	Spratelloides_lewisi*	0	50	6	herring
sp_100	Spratelloides_robustus	0	50	12	herring
sp_101	Thryssa_aestuaria	0	50	13.8	anchovy
sp_102	Thryssa_baelama	0	50	16	anchovy
sp_103	Thryssa_brevicauda*	0	50	7.5	anchovy
sp_104	Thryssa_dayi*	0	50	21.5	anchovy
sp_105	Thryssa_dussumieri	0	50	11	anchovy
sp_106	Thryssa_encrasicholoides	0	50	10.7	anchovy
sp_107	Thryssa_hamiltonii	10	13	27	anchovy
sp_108	Thryssa_malabarica*	0	50	17.5	anchovy
sp_109	Thryssa_mystax	0	50	15.5	anchovy
sp_110	Thryssa_purava	0	50	15.5	anchovy
sp_111	Thryssa_setirostris	1	20	18	anchovy
sp_112	Thryssa_spinidens*	0	50	16.5	anchovy
sp_113	Thryssa_vitrirostris	0	50	20	anchovy

Table S02 Earth System Models used for each variable analysed. We considered only models that provided the complete series of data from 1860 to 2100 under the historical, RCP 2.6 and RCP 8.5 experiments. The variables analysed included sea surface temperature (CMIP5 variable name 'TOS', in K (converted to ºC in this study)), sea surface salinity ('SOS', in psu), total chlorophyll mass concentration at surface ('Chl', in kg m^{-3}), dissolved oxygen concentration at surface ('O_2', in mol m^{-3}) and pH at surface ('pH', in mol H kg^{-1}).

MODELLING CENTER	COUNTRY	MODEL	Chl	O_2	pH	SOS	TOS
BCC	China	BCC-CSM1-1					x
		BCC-CSM1-1-m					x
CCCma	Canada	CanESM2	x		x	x	x
NCAR	USA	CCSM4				x	x
NSF-DOE-NCAR	USA	CESM1(CAM5)				x	x
CNRM-CERFACS	France	CNRM-CM5	x	x	x	x	x
CSIRO-QCCCE	Australia	CSIRO-Mk3.6.0				x	x
FIO	China	FIO-ESM					x
NOAA GFDL	USA	GFDL-CM3				x	x
NASA GISS	USA	GISS-E2-H				x	x
		GISS-E2-R				x	x
MOHC	UK	HadGEM2-AO				x	x
		HadGEM2-ES	x	x		x	x
IPSL	France	IPSL-CM5A-LR	x	x	x	x	x
MIROC	Japan	MIROC5				x	x
		MIROC-ESM	x		x	x	x
		MIROC-ESM-CHEM	x		x	x	x
MPI-M	Germany	MPI-ESM-LR	x	x	x	x	x
		MPI-ESM-MR	x	x	x	x	x
MRI	Japan	MRI-CGCM3					x
NCC	Norway	NorESM1-M				x	x
TOTAL MODELS			8	5	7	17	21

4.6.2 Additional References

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CHAPTER 5

5. FINAL REMARKS AND FUTURE PERSPECTIVES

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5.1 Final remarks

The main goal of this thesis was to characterize global patterns and forecast the effects of climate change on marine biodiversity. Overall, the work presented here provides: i) a comprehensive overview on climate change in marine environment; ii) an unique application of Ecological Niche Models in marine realm; iii) an overview of marine global patterns of diversity; iv) an insight in how predicted climate change may impact marine biodiversity at a global scale; v) an outlook of critical areas for global fisheries that require closer attention on climate change scenario.

Chapter 2 explores the impacts of climate change on coastal lobster distribution and possible effects on fisheries world-wide**.** This study shows that potential losses in richness for lobster species were mainly projected in areas with high commercial fishing interest, with species projected to contract their range between 40% and 100%, in response to climate change. Spiny lobsters higher losses were projected in the coasts of wider Caribbean region/Brazil, eastern Africa and Indo-Pacific area, areas with several directed fisheries and aquacultures. While clawed lobsters were projected to shifts their range to northern latitudes likely affecting the North European, North American and Canadian fisheries. Lobsters represent an important resource for local and global economies, so understanding how they might be affected by climate change scenarios is paramount for developing specific or regional studies.

The patterns of cephalopod coastal diversity and potential changes under climate change in richness, mean body size and assemblage composition were evaluated in **Chapter 3.** This study presents an end-century scenario with 96% of cephalopod species predicted to experience range contraction and 15% completing losing their environmental space. Nestedness was projected to be the main driver of species compositional change and no significative differences in projected maximum body size were found. Fisheries in countries at higher latitudes might benefit from the projected shifts, although the search of refugia of smaller tropical species might potentially lead to a mitigation of the negative effects of climate change in these areas. These findings reflect major climatic drivers of change and highlight the idea that even though cephalopod species seem good candidates to replace overexploited fish stocks in the near future, they may not have the environmental space to do so.

In **chapter 4** the impacts of climate change in small pelagic fish species (SPF) richness, catch potential and geographic range size was analyzed. The study shows that between 45% and 46% of the current habitat of SPF species could lose its suitability, under a range of mitigation scenarios, by the end of the century. In turn, catch potential was projected to decline 32% to 44%, under strong and moderate mitigation scenarios. Between 77-93% of the species were projected to shrink their geographic range and shift their mean latitudes poleward. Given the ecological importance of SPF species (anchovies, herrings and sardines) and that the economies of many coastal countries are highly dependent on them, presented results highlight the need for precautionary management that can easily adapt to projected changes.

The results obtained have broad implications and provide critical information to anticipate negative impacts of climate change on marine biodiversity. Providing global assessments that can be taken into account when orienting local or specific fragilities of marine biodiversity to climate. Nevertheless, geographic and taxonomic responses to climate change are highly variable and several key aspects on the distribution of biodiversity in the oceans of tomorrow remain to be addressed.

5.2 Future Perspectives

Research of climate change impacts in marine biodiversity is still lagging behind that made in terrestrial environment. To guide the scope of future studies addressing the responses of species to changing ocean conditions several factor should be taken into account.

Recent advances in observational data collection and access to large marine environmental databases provide an improved foundation for statistical ecological niche models. But do not address structural uncertainties in models that arise from incomplete understanding of species interactions and physiological thresholds. This level of knowledge would instead require a shift from reliance on correlations between marine species and their environment, toward models that more clearly establish functional relationships with the physical and biological underpinnings of habitat utilization. These relationships could yield the development of process-based models, rooted in ecological understanding (Palacios *et al.*, 2013; Koenigstein *et al.,* 2016); or mechanist models, based on physiological understanding (Kearney & Porter, 2009; Kearney *et al.*, 2010; Enriquez-Urzelai *et al.,* 2019); or food web models, based on biological knowledge (Gravel *et al.*, 2013; Albouy *et al.,* 2019). Or better yet, hybrid models that incorporate a range of ecological, physiological and biological information to define the fundamental niche of the species models are aimed for.

The coarse resolution of CMIP5 climate models limit the ability to predict finer processes affecting species distribution, such as stratification or variation in coastal currents that can significantly impact larval dispersal patterns and other processes. Recent high-resolution climate projections (Saba *et al.,* 2016) or dynamical downscaling of CMIP5 (McSweeney *et al*., 2014) show promising results when applied in regional studies and can contribute to reduce uncertainty in ENMs projections.

Fisheries face a serious new challenge as climate change drives marine animals to shift their geographical range to new territories, crossing national and other political boundaries in the coming decades and creating the potential for conflict over newly shared resources (Pinsky *et al.*, 2018). But fisheries data is subjected to high uncertainty due to unreported catches, discards, geographical bias on catches report, among other things. So recent improvements in spatial allocation procedures that allow a reconstruction of catch data (from 1950 to 2010) for all countries in the world, can widely assist the debate about the role of fisheries in a global framework as well as in national food security settings (Zeller *et al.*, 2016).

Potential for adaptation to new forthcoming conditions is also something lagging in climate change research, as already stated by Darwin (1859) "*It is not the strongest of the species that survives, nor the most intelligent that survives. It is the one that is the most adaptable to change*". Predicting the effects of climate change on marine populations depends not only on assessing the effects of climate stressors on performance, but also on the potential for adaptation through genetic changes (Munday, 2014).

Future efforts will be focus on addressing these topics as a way to improve species distribution models projections, to guide regional studies and advise actions to help endangered and commercially important marine species to adapt to the threat of climate change. Yet, it is inevitable not to be aware and to think that further efforts to reduce global anthropogenic CO_2 emissions by nations could help to perpetuate and preserve species persistence in tomorrow's ocean.

5.3 References

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