



Climate change impacts on the distribution of coastal lobsters

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Received: 17 January 2018 / Accepted: 26 October 2018 / Published online: 16 November 2018
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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 shift 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.

Introduction

Climate change, overfishing and habitat degradation are the main reasons for the drastic decline of marine populations over the past 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 and Wahle 2013). World lobster trade more than doubled over the past 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

Responsible Editor: F. Bulleri.

Reviewed by Undisclosed experts.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00227-018-3441-9>) contains supplementary material, which is available to authorized users.

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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 and Cheung 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.

Methods

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 points data in a worldwide $1^\circ \times 1^\circ$ 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 Enoplometopidae) (Electronic 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 barbareae*)—corresponding to those with fewer than 20 records over the study area (Wisiz 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 (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 (Electronic 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 is the one that projected the raise in surface temperature by the end-century closer to the + 1.5 °C increase targeted by the Paris Agreement (United Nations 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 $1^\circ \times 1^\circ$ 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 (Tebaldi and Knutti 2007; Electronic supplementary material Fig. S01).

Ecological niche modelling

In order to constrain algorithmic uncertainty associated with ecological niche models (ENM's) we implemented an ensemble forecasting method (Araújo and 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 five 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 and 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 data were representative of the whole water column. 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 for these groups (Fig. 2). Changes were also quantified for the genera with higher economic relevancy 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.

Results

Present patterns in coastal lobster distribution

Richness for coastal lobster species was projected to peak around 14° S (mean HS 49 ± 11 species) and 9° N latitude (Fig. 1a— 37 ± 13 species) in the baseline period. When

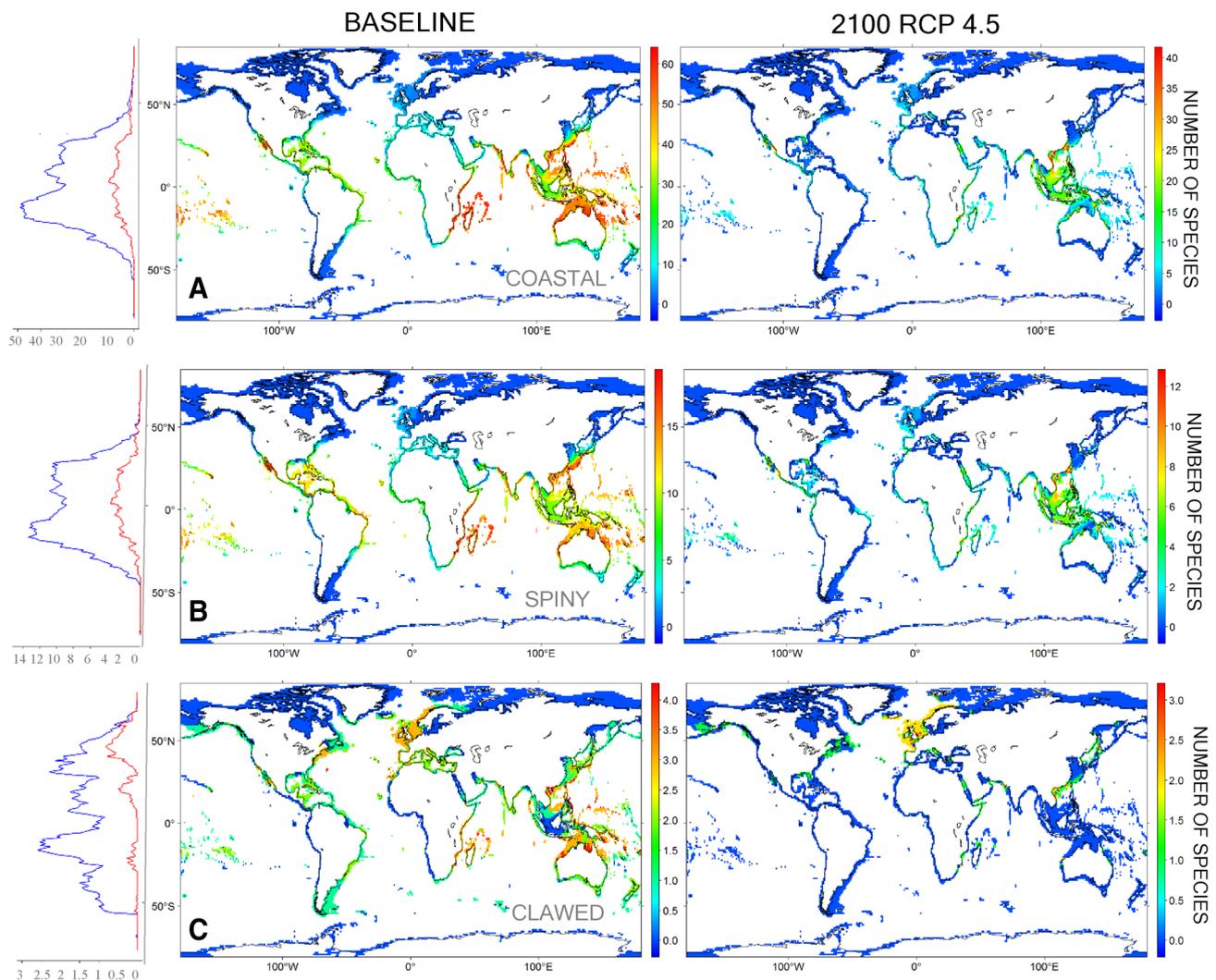


Fig. 1 Predicted species richness for **a** coastal lobster assemblage, **b** spiny lobster and **c** clawed lobster families, in the baseline and end-century periods, under the RCP 4.5 scenario. Left panel shows mean

species richness predicted per latitude for the baseline period (blue line) and end-century (red line) scenario

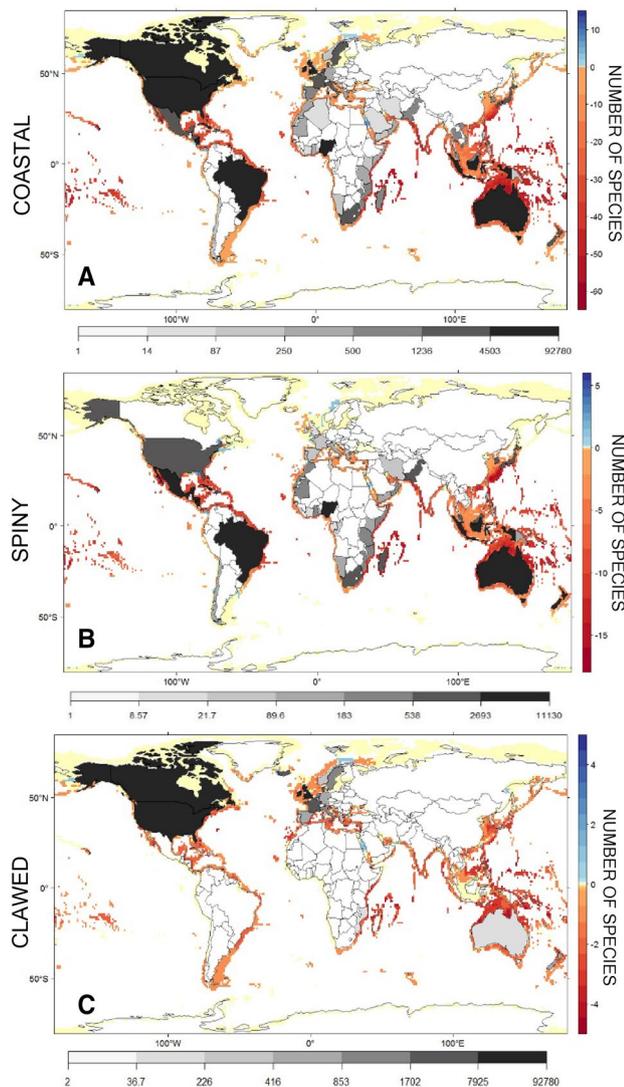


Fig. 2 Predicted changes in species richness for **a** coastal lobster assemblage, **b** spiny lobster and **c** clawed lobster families, between baseline and end-century periods, under the RCP 4.5 scenario. In land shades of grey represent coastal lobster* global capture production per country [* see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

looking at the major coastal families, we found that spiny lobsters' species projected richness peak is around 18°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 9°N (11 ± 3 species), once again influenced by *Panulirus* species present on the wider Caribbean region (Fig. 1b). Clawed lobsters' species projected richness peaks around 17°S (3 ± 1 species), driven by the North Australian lobster diversity and 33°N (2 ± 1 species), mainly due to genera *Homarus* and *Nephrops* (Fig. 1c).

Projected changes in coastal lobster distribution

Projected losses in diversity for coastal lobster species occurred mainly in the tropical zone (between 18°S and 20°N), with species projected to contract their climatic envelope 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.

Projected losses in diversity for spiny lobsters species 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 and 100% envelope contraction) in areas as south Africa (*J. lalandii*), south Australia and New Zealand (*J. edwardsii*) coasts (Fig. 3b). Regarding clawed lobsters, our models project an envelope contraction of about 71% for *H. americanus*, 44% for *H. gammarus* and 58% for *N. norvegicus*, with all species projected to suffer a shift north and loss of suitable habitat in the southern range (Fig. 3c, d).

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 climatic 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

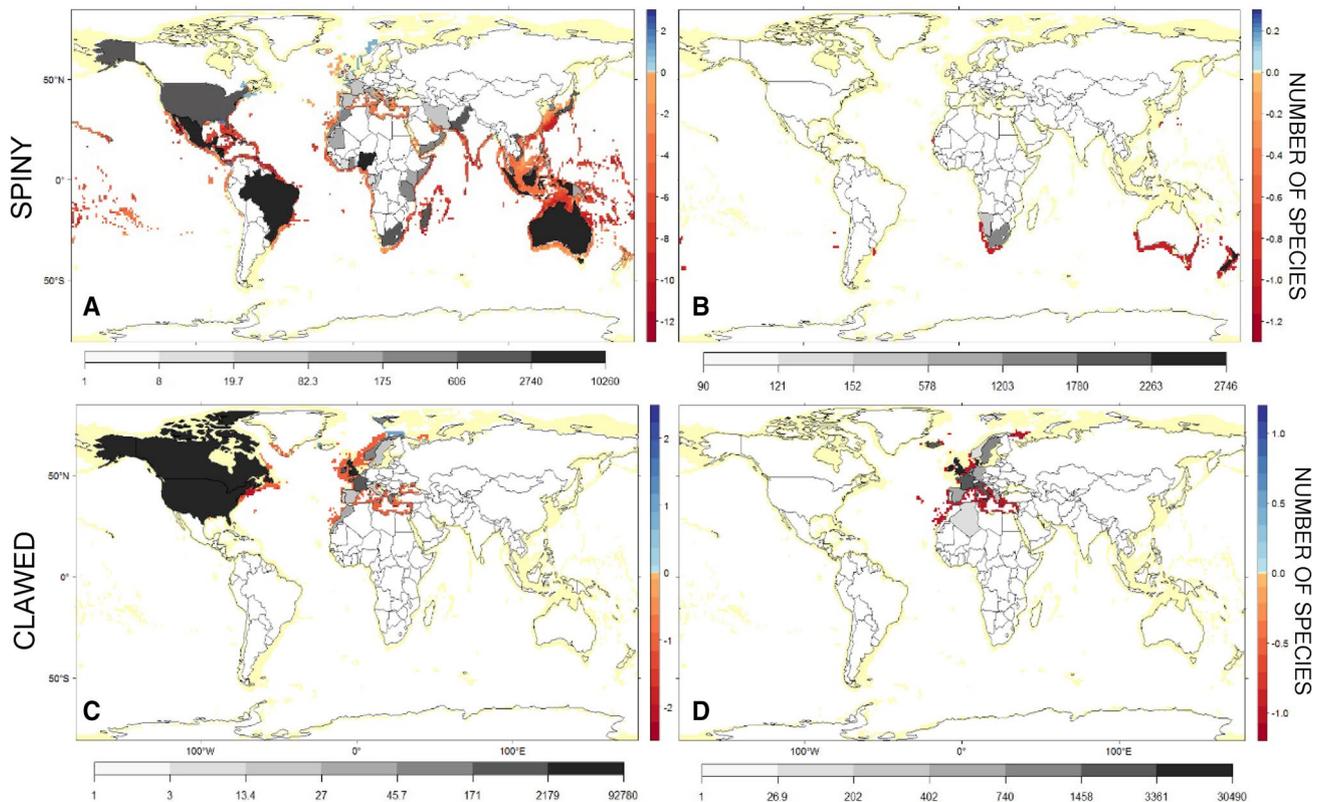


Fig. 3 Projected changes in species richness for the coastal lobster genera with commercial relevancy **a** *Panulirus*, **b** *Jasus*, **c** *Homarus* and **d** *Nephrops*, between the baseline and end-century periods, under

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), 5]

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), revenue 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.

Clawed lobsters are much less speciose, yet highly valuable, with only three 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 HS in the southern range (Fig. 3c, 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 is 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 and Cheung 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 variables that better correlate with species distribution (Harley et al. 2006), but factors like ocean acidification have proved 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 refer 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 of HS 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 losses of suitable habitat 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 (Hoffmann and 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).

Acknowledgements The authors would like to thank the IUCN Red List and its partners, namely Prof. Kent Carpenter, Dr. Ben Collen and Dr. Monika Bohm for collecting and sharing the data on lobster's distribution. We acknowledge the World Climate Research Programme's Working Group on Coupled Modelling, which is responsible for CMIP, and we thank the climate modelling groups (listed in Table S02) and also Dr. Richard Wahle and other anonymous referees for useful comments. The Portuguese Foundation for Science and Technology (FCT) supported this study through a PhD grant (SFRH/BD/51514/2011) to JBP and a Senior Research Position (FCT Development Grant 2013) to RR. MBA acknowledges the Integrated Program of IC&DT Call no. 1/SAESCTN/ALENT-07-0224-FEDER-001755 for support of his research.

Compliance with ethical standards

Conflict of interest All authors declare they have no conflict of interest.

Ethical approval This article does not contain any studies with animals performed by any of the authors.

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