ORIGINAL ARTICLE

On the need to consider multiphasic sensitivity of marine organisms to climate change: a case study of the Antarctic acorn barnacle

Ramón Gallego[1,2]*, Todd E. Dennis[2], Zeenatul Basher[2,3], Shane Lavery[2] and Mary A. Sewell[2]

[1]School of Marine and Environmental Affairs, University of Washington, Box 355685, Seattle, WA 98195-5685, USA, [2]School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland Mail Centre, Auckland 1142, New Zealand, [3]Center for Systems Integration and Sustainability, Michigan State University, 115 Manley Miles Bldg, East Lansing, MI 28823, USA

ABSTRACT

Aim Species distribution models (SDMs) are routinely employed to evaluate shifts in the geographic distributions of organisms in response to changing climatic conditions. Many marine invertebrates exhibit a biphasic life cycle: benthic adults and planktonic larvae, which inhabit different environments and may react dissimilarly to anticipated changes in climatological patterns. To date, SDMs applied to benthic species have only considered adult life-history stages. Here, we present the first study in which SDMs have been simultaneously developed for both the larval and adult stages of the same organism.

Location The Southern Ocean.

Methods Occurrence data for the study species, the Antarctic barnacle *Bathylasma corolliforme*, were sourced from: (1) benthic geo-referenced records from museum collections and online databases; and (2) observations of planktonic larvae identified with genetic and morphological methods. These records were used to construct two independent SDMs (adult-larvae) with Maxent 3.3.3k; their outputs were then projected to environmental conditions forecast for the year 2050 (IPCC scenario A1B).

Results The two different SDMs had high predictive capability and identified preferred environmental conditions of each life-history stage. For the projected 2050 climate change scenario, SDMs predicted that the extent of environmentally suitable areas of both life-history stages was reduced, with planktonic larvae experiencing greater reductions and latitudinal displacement of their suitable areas.

Main conclusions For multiphasic species, considering only a single life-history stage while studying distribution shifts may lead to erroneous conclusions for the species as a whole, regardless of the predictive capability of models employed. Ignoring the changes in suitable areas for larval stages can lead to underestimation of habitat reduction, distribution shifts, effects on population connectivity and potential for colonization of newly available habitats.

Keywords
benthos, climate change, distribution shifts, larvae, marine, Maxent, species distribution models

*Correspondence: Ramón Gallego, School of Marine and Environmental Affairs, University of Washington, Box 355685, Seattle, WA 98195-5685, USA.
E-mail: rgallego@uw.edu

INTRODUCTION

It is now generally accepted that anthropogenic emissions of greenhouse gases are changing global climate conditions, which affects marine biomes through changes in the temperature, salinity and acidity of seawater, and in ocean circulation and sea-ice extent (IPCC, 2007; Turner *et al.*, 2009). Such changes impair physiological processes, increase mortality, and alter distribution ranges and reproductive phenology (Beaugrand *et al.*, 2002; Edwards & Richardson, 2004). Studies on holoplanktonic and benthic organisms have reported shifts in species' geographic ranges associated

with ocean warming, resulting in constriction of suitable area (Sequeira *et al.*, 2014), intrusion of temperate species into higher latitudes (Beaugrand *et al.*, 2002), or show the opposite effect in areas where regional cooling has occurred (Beaugrand *et al.*, 2002).

Benthic species typically disperse through planktonic larvae, and have been the focus of many thermal- and acidification-sensitivity experiments, ranging from fertilization success to larval survival rates (reviews: Byrne, 2011, 2012; Przeslawski *et al.*, 2015). There have, however, been only three recent studies which have highlighted the importance of larval stages in climate-related adult range expansions (Kirby *et al.*, 2007; Banks *et al.*, 2010; Byrne *et al.*, 2016). In the echinoid *Echinocardium cordatum*, a range increase and higher population density of adults in the North Sea is a consequence of both increased larval numbers and higher adult survival during winter months (Kirby *et al.*, 2007). The range expansion and connectivity patterns of the sea urchin *Centrostephanus rodgersii* was linked with an increase on the poleward flow of a warm current (Turner *et al.*, 2009). Similarly, the potential of the asteroid *Asterias amurensis* to invade the Southern Ocean is dependent on the presence of a similar benthic environment for the adults and a surface warming that would increase larval dispersal towards the poles (Byrne *et al.*, 2016).

Species distribution models (SDM) are useful tools to estimate not only the potential geographic range of a species (Reiss *et al.*, 2011) but also to predict range changes in response to past or future environmental conditions (Basher & Costello, 2016). Such models have been applied to benthic and holoplanktonic species. However, to date no study has attempted to develop a SDM for both the benthic and planktonic stages of the same species, as suggested by Dambach & Rödder (2011). An obvious reason for this omission is the scarcity of larval records, due to the difficulties of identifying larvae to species level. A clear advantage of modelling both life stages is that not only are estimates of the potential range of each life stage generated but also insights regarding how changes in the environment differentially affect each life stage. Biological responses to global climate change will not necessarily be the same for adults and larvae, a critical issue that may be overlooked if only one life stage is studied.

Here we present the first study in which two SDMs – one for each life stage – have been generated for the same species, the acorn barnacle *Bathylasma corolliforme* (Hoek, 1883). This species, which is endemic to the Southern Ocean, lives on rocky bottoms at depths from 100 to 1600 m, where it feeds on particulate material suspended by bottom currents (Dayton *et al.*, 1982). *Bathylasma corolliforme* is one of the most characteristic species of the hard-substrate faunal assemblages in the Ross Sea (Smith *et al.*, 2007), and shell plates from *B. corolliforme* constitute the only sediment on large areas of the sea bottom [e.g. the north-west Ross Sea at the edge of the continental shelf (Bullivant & Dearborn, 1967)].

The two life stage-specific SDMs presented in this study were produced with complementary research objectives: first, to investigate if suitable areas for larvae and adults will change in response to climatic conditions forecast for the year 2050; and second, to demonstrate the necessity of considering changes in environmentally suitable areas for larvae when assessing distribution range shifts in benthic species.

MATERIALS AND METHODS

Observation records

Species distribution models were generated using presence-only records of adult and larval *B. corolliforme*. Adult records were obtained from a variety of online databases [Ocean Biogeographic Information System (OBIS, www.iobis.org), Global Biodiversity Information Facility, Scripps Institution of Oceanography and Australian Antarctic Centre, accessed in January 2013], the New Zealand National Institute of Water and Atmospheric Research (NIWA) Invertebrate Collection and publication records (Full list in Appendix S1 in the Supporting Information).

Generation of larval databases relies on the ability to identify specimens to the species level. Morphological identification of *B. corolliforme* larvae has been tentatively suggested in previous Antarctic studies (Foster, 1989; Scheltema *et al.*, 2010), as it is the only known acorn barnacle from the Southern Ocean. More recently, we have used genetic markers with species-level resolution (ribosomal 16S and cytochrome oxidase subunit 1) and phylogenetic tree reconstruction (see Fig. S1.2) to positively identify *B. corolliforme* larvae (Gallego *et al.*, 2014). During this procedure, we also were able to detect the presence of *Verrucomorpha* nauplii among the more abundant *B. corolliforme* larvae. Thus, we only used records identified using molecular means or those with correlated morphology in which the authors' expertise allowed them to positively identify the nauplii as balanomorph larvae; and discarded records referring more broadly to cirriped nauplii or cyprid.

To mitigate the effects of spatial autocorrelation on presence data (Boria *et al.*, 2014) produced by the over-representation of highly surveyed localities, we trimmed the dataset with the spatial rarefaction tool implemented in the SDMtoolbox for ArcGIS (Brown, 2014) and selected points at least 10 km apart. This way, the larval SDM used observations from 62 localities (from the 72 available), while the adult model included observations from 43 localities (56 originally), well above the minimum number of localities needed for Maxent 3.3.3k (Phillips *et al.*, 2006) to construct a reliable model (Pearson *et al.*, 2007). The locations of the records that were included in our model and the list of publications used and discarded are provided in Appendices S1 and S2.

Environmental layers

Different sets of environmental layers (5 arc-minute-resolution) were selected to create the best possible SDM for each of the two life-history stages, based on previous studies of the

biology of *B. corolliforme* (Dayton *et al.*, 1982) and on Antarctic meroplankton (Shreeve & Peck, 1995; Edwards & Richardson, 2004). Given the endemic character of this species to the Southern Ocean, all environmental layers were constrained on their northern limit to the Polar Front. To generate the SDM for larvae, we used annual means of sea-surface salinity and temperature, while the adult SDM was constructed from annual means of near-sea-floor values for these two factors. Both models included annual mean sea-ice coverage and bathymetry; benthic models also incorporated a slope layer, generated from the bathymetry layer using the SLOPE module in the Spatial Analyst toolbox from ARCMAP 10.1 (ESRI, Redlands, CA, USA). To predict changes in geographic distribution of the two different life stages in response to potential future climate change scenarios, year 2050 (IPCC scenario A1B) estimations of mean sea-ice coverage, salinity and temperature layers (at the relevant surface or bottom depth) were incorporated. A comprehensive list of all environmental layers, their source and maps of their variation across the study area are included in Table S1.2 and Fig. S1.3.

Statistical relationships between environmental variables were assessed using Pearson's product-moment correlation ('r'), as highly collinear variables will negatively affect SDMs and the transferability of their predictions (Jiménez-Valverde *et al.*, 2009; Dambach & Rödder, 2011). All environmental layers included in adult models had r-values ≤ 0.60, whereas for the larval models r-values ≤ 0.52, well below the suggested threshold values of 0.75 (Cord & Rödder, 2011).

To avoid the effect of decreasing cell size with increased latitude (Elith *et al.*, 2011), and thus a bias on background selection towards the poles, all environmental layers were transformed from the original WGS 1984 coordinate system to the South Pole Azimuthal Equal area projection with a cell size of 75.98 km^2 using the SDMtoolbox available for ARCGIS (Brown, 2014).

Model development

SDMs were developed independently for each life stage using MAXENT. Each model was constructed in a two-step process using the spatial jackknife approach implemented in the SDMtoolbox. For each life stage, the rarefied occurrence data was first split into three spatially discrete bins – as were the background points – and models were created by using two bins as training data and the remaining as test data. Using these bins, the 'ENMeval' package (Muscarella *et al.*, 2014) implemented in R 3.3.0 was used to select the best SDM possible for each life stage, allowing for different combinations of background selection, MAXENT feature complexity and the penalty applied for overfitting solutions. The settings that produced the model with the lowest Akaike information criterion corrected for small sample size (AICc) – which reflects the best combination of model complexity and goodness-of-fit (Warren & Seifert, 2011) – were used in a second step to generate two SDMs (larva and adult) in which the full set of presence points and 10,000 background points were used.

The predictions of these two models were projected to the full extent of the Southern Ocean in present and future (year 2050) climate conditions. In each SDM, every 75.98 km^2 cell was defined as suitable if the MAXENT output was greater than the 10 percentile threshold, defined as the value of the model logistic output for the training set after discarding the lower 10% (Radosavljevic & Anderson, 2014). If a cell classification changed from being suitable to unsuitable between present and future scenarios, this was considered as 'habitat loss'; and similarly as 'habitat gain' if the opposite occurred. Suitable habitat areas were plotted as a function of latitude, in both present and future (2050) scenarios, and presented as mean suitable areas.

SDM performance was evaluated using the 'ENMeval' and 'ENMtools' (Dan Warren, personal communication, available from github.com/danlwarren) R packages with a suite of indices, including the standard index of 'area under the curve' (AUC), which ranges between 0 and 1; '1' being perfect discrimination between background and presence points and 0.5 indicating the model is no better than random (Fielding & Bell, 1997). Two indices were employed to estimate the degree of model overfitting: the omission rate, which indicates the proportion of test localities with suitability lower than the 10 percentile threshold (Radosavljevic & Anderson, 2014); and the difference between AUC in training and test data (Warren & Seifert, 2011). A complementary view on the degree of overfitting was obtained by plotting the predicted model suitability and location of presence data in the environmental space, using the visualize.enm tool from ENMtools.

The relative importance of each environmental variable that was included in the models was measured in three complementary ways: (1) variable contribution was calculated using the percentage of model gain as each variable was sequentially added to the model; (2) variable predictive capability was assessed by performing jackknife tests which compared the training gain of the *full* SDM with that of two different SDMs: one generated with a single variable (i.e. how well does a model would perform with just that variable?) and a second SDM where the variable was excluded (i.e. how much predictive capability was lost?); (3) model sensitivity to each variable was examined by plotting model response curves over the range of each environmental variable, while holding the remaining variables constant.

Model reliability

The SDM approach we have presented here highlights hidden risks faced by the acorn barnacle *B. corolliforme,* by considering larval sensitivity to environmental conditions through a spatial perspective. The predictive capability of models is limited, and caution should be taken when interpreting their output. However, given the very limited information available on the larval biology of most Antarctic marine fauna, the application of SDMs to adult and larval stages applied here represents a unique way of addressing the effects of climate change on species' distributions.

Many factors affect the reliability of SDM, and a primary concern of presence-only modelling lies with bias of sampling effort (Elith *et al.*, 2011), which can lead to oversensitivity of model results to local conditions (Yackulic *et al.*, 2012). We addressed this problem differently for adults and larvae. For adults, we followed the procedures recommended by Ponder *et al.* (2001) of creating a bias grid from a separate target group. Benthic polychaetes were selected as the target group because they are abundant, ubiquitous (Brandt *et al.*, 2007), easy to identify to Class level, and typically collected using similar sampling techniques to *B. corolliforme* adults. Records were extracted from OBIS, and due to the large number of species included, counts per grid cell were transformed [$\log_{10}(x + 1)$], thus giving a grid that conformed with Maxent requirements (values from 1 to max) and accurately reflected the differences in sampling effort (Phillips *et al.*, 2009). However, this approach was not appropriate for larvae, as most of the presence points were located in the Antarctic Peninsula and not in the Ross Sea. Applying such a bias grid would have only amplified the issue we intended to mitigate. In this case, we implemented a background selection mask based on distances from the same observation points used in SDM construction (Local Adaptive Convex-Hull, from SDMtoolbox) and used 100, 200, 300 and 400 km from observation points as possible backgrounds.

RESULTS

We generated two SDMs (larval and adult) to estimate changes in environmentally suitable areas with near-future climate conditions (2050, IPCC fourth report, scenario A1B).

Adult SDM

The SDM generated for the adult (benthic) population of *B. corolliforme* exhibited high predictive performance (area under the curve, AUC = 0.9704), without showing any signs of overfitting: the model presented a low difference in AUC between test and training points (0.029), a low omission rate (0.013) and the suitability across the environmental space did not concentrate around presence points (see Fig. S3.4). Ocean depth was found to be the most important environmental variable (*c.* 75%), followed by sea bottom salinity (*c.* 9.5%) and sea-ice coverage (*c.* 8%), as highlighted by model composition and response curves (see Fig. S3.4).

Under current climatic conditions, our model predicted high environmental suitability for adult *B. corolliforme* on shelf-break areas surrounding the Antarctic continent between 65 and 72° S (Fig. 1a), and around offshore islands throughout the Southern Ocean. Under the 2050 predicted climate change scenario, the area of environmental suitability of shelf-break areas for adult *B. corolliforme* is reduced in the Ross and Weddell Seas; in waters surrounding some offshore islands at lower latitudes (*c.* 50–55° S), the adult model forecast an increase in environmental suitability (Figs 1b & 2). However, the vast majority of shelf areas remain suitable habitat for adult *B. corolliforme* in both present and future scenarios (Fig. 1c).

Larval SDM

The larval (planktonic) SDM showed a high predictive capability (AUC score of 0.889) and while the difference in AUC between training and test data was higher than for adults (0.15 vs. 0.028), the low complexity of the model allowed for a spread-out distribution of the suitability in the environmental space (see Fig. S3.5). The model relied primarily on ocean depth, sea-ice coverage and sea-surface temperature – variables that all showed sharp response curves and high contributions (see Fig. S3.5). Highest suitability was predicted for shallow, ice-free areas with temperatures between −2 and 0 °C. Environmental suitability under current climatic conditions was higher in the West Antarctic Peninsula, the Ross Sea Shelf, the Scotia Arc and the Kerguelen Plateau (Fig. 3a).

Comparison of the larval and adult SDMs suggests that connectivity among adult benthic populations in shelf-break areas occurs via the Antarctic coastal countercurrent, whereas the role of the most important circulatory pattern in the Southern Ocean, the Antarctic Circumpolar Current, is limited to the Scotia Arc, the Kerguelen Plateau and the waters to the north-west of the Ross Sea (Fig. 3b).

Under the climate change scenario predicted for 2050, larval distribution shifts are very different from those of adults: environmental suitability is greatly reduced at both high and low latitudes (Fig. 4). In the High Antarctic (*c.* 73°–78° S), and particularly in the Ross Sea, this loss is likely linked to the predicted increase in sea-ice extension. Generally, suitable habitat is shifted towards mid-latitudes, mainly in the Bellingshausen Sea and the West Antarctic Peninsula (60°–72° S). Importantly, the suitability around the Antarctic Peninsula changes significantly: The northern end of the Peninsula faces a decrease in suitable area, particularly towards the Scotia Arc, while environmental suitability is increased in the south-east, from the end of the Peninsula to the shelf waters on the Bellingshausen Sea.

As with any models, the larval and adult SDMs presented here should be viewed with some degree of caution, particularly when projecting to different space(s) and time(s).

Figure 1 Species distribution model (SDM) generated with Maxent for *Bathylasma corolliforme* adults. (a) Relative suitability on the Southern Ocean region for present conditions. Double dotted lines limit the Antarctic Circumpolar Current. (b) Relative suitability projected to the 2050 scenario. (c) Change in environmentally suitable areas for the year 2050. White areas remain unsuitable in present and future scenarios, green areas remain suitable and orange and purple areas denote transitions from non-suitable to suitable and vice versa.
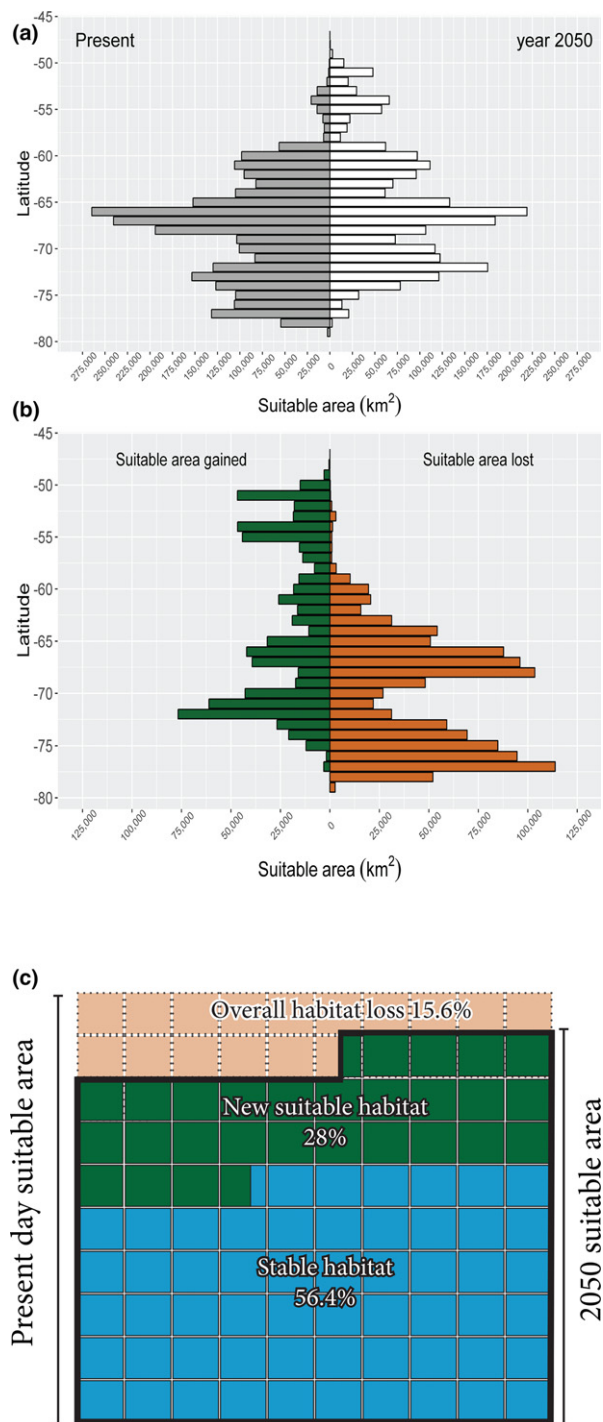
Present time

2050

Changes in suitable areas
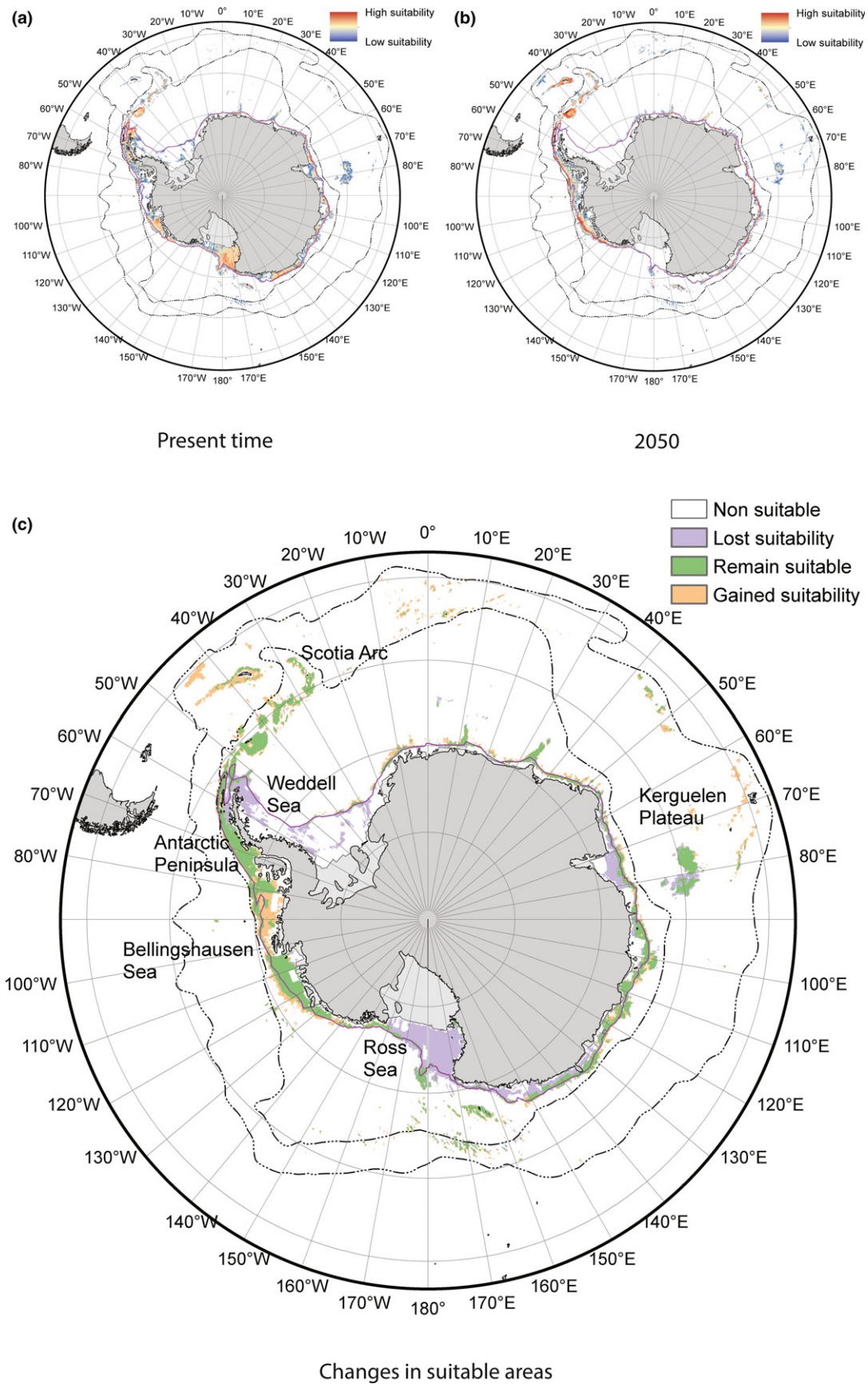
Figure 2 Total area found environmentally suitable for *Bathylasma corolliforme* adults in the Southern Ocean. (a) Present and near-future (2050) scenario suitable area, plotted as function of latitude. (b) Total habitat gain (areas found environmentally unsuitable in the present scenario but suitable in the 2050 scenario) and habitat loss (from suitable to unsuitable). (c) Portrayal of the change in total suitable areas for *B. corolliforme* adults, as percentage of the present scenario, showing total habitat loss and percentages of new and stable habitat.

However, in the SDMs for both life stages, we not see evidence for model overfitting to present conditions, and the environmental predictors for areas of lost suitability had values within the training range, i.e. the conditions in the year 2050 were not "new" to the model and thus the predicted change in suitability is considered to be credible.

DISCUSSION

Model composition

The SDM constructed for the adult stages greatly depended on depth; a key environmental factor influencing the geographic distribution of cold-water benthos (Davies & Guinotte, 2011; Reiss *et al.*, 2011; Pierrat *et al.*, 2012). In *B. corolliforme*, which has an exoskeleton made of calcite plates (Burgess *et al.*, 2010), the depth limit may be related to the difficulty of producing calcium carbonate ($CaCO_3$) beneath the carbonate compensation depth (CCD), the point below which $CaCO_3$ deposition is less than the rate of dissolution (Griffiths, 2010). Maximum CCD in the Southern Ocean is in the 4000 m range (Mackensen *et al.*, 1990), similar to the maximum depth from which the response curves of the adult model approach values near 0 (see Fig. S3).

Sea-ice extension was also found to be a crucial factor for the adult SDM. Previous studies have suggested an important contribution of this factor to the predicted distribution of benthic invertebrates from Antarctic shelf areas (Pierrat *et al.*, 2012). Although the influence of sea-ice on benthic organisms is more direct and pronounced in species that exclusively feed on phytodetritus (Smith *et al.*, 2008), more generalist feeders – such as *B. corolliforme* – may be affected through the sinking of sea-ice infauna to the benthos (Gradinger, 2001).

Importantly, the SDM generated for larvae included an additional factor, sea-surface temperature. Temperature is the environmental feature which shows a higher impact on larval development, affecting larval swimming performance, metabolic rate and planktonic larval duration (see review in Byrne, 2011). Laboratory experiments have shown how moderate increases in temperature result in beneficial effects, with shorter developmental times and reduced PLD – which entails lower rates of larval mortality (Rumrill, 1990) – while higher temperatures generally involve deleterious effects. The temperature threshold for such divergent effects is dependent on adult thermal range, and high latitude species present greater sensitivity to temperature increases (Peck *et al.*, 2014). Furthermore, for planktotrophic larvae, maintaining higher metabolic rates as temperature rises depends on access to suitable food sources, which in *B. corolliforme* might be strongly linked with changes in sea-ice extension: sea-ice coverage is a key factor shaping phytoplankton assemblages in the Southern Ocean (Smith *et al.*, 2014) and ice-free areas host diatom blooms, the preferred food source for barnacle larvae (Gaonkar & Anil, 2010). On the other hand, sea-ice
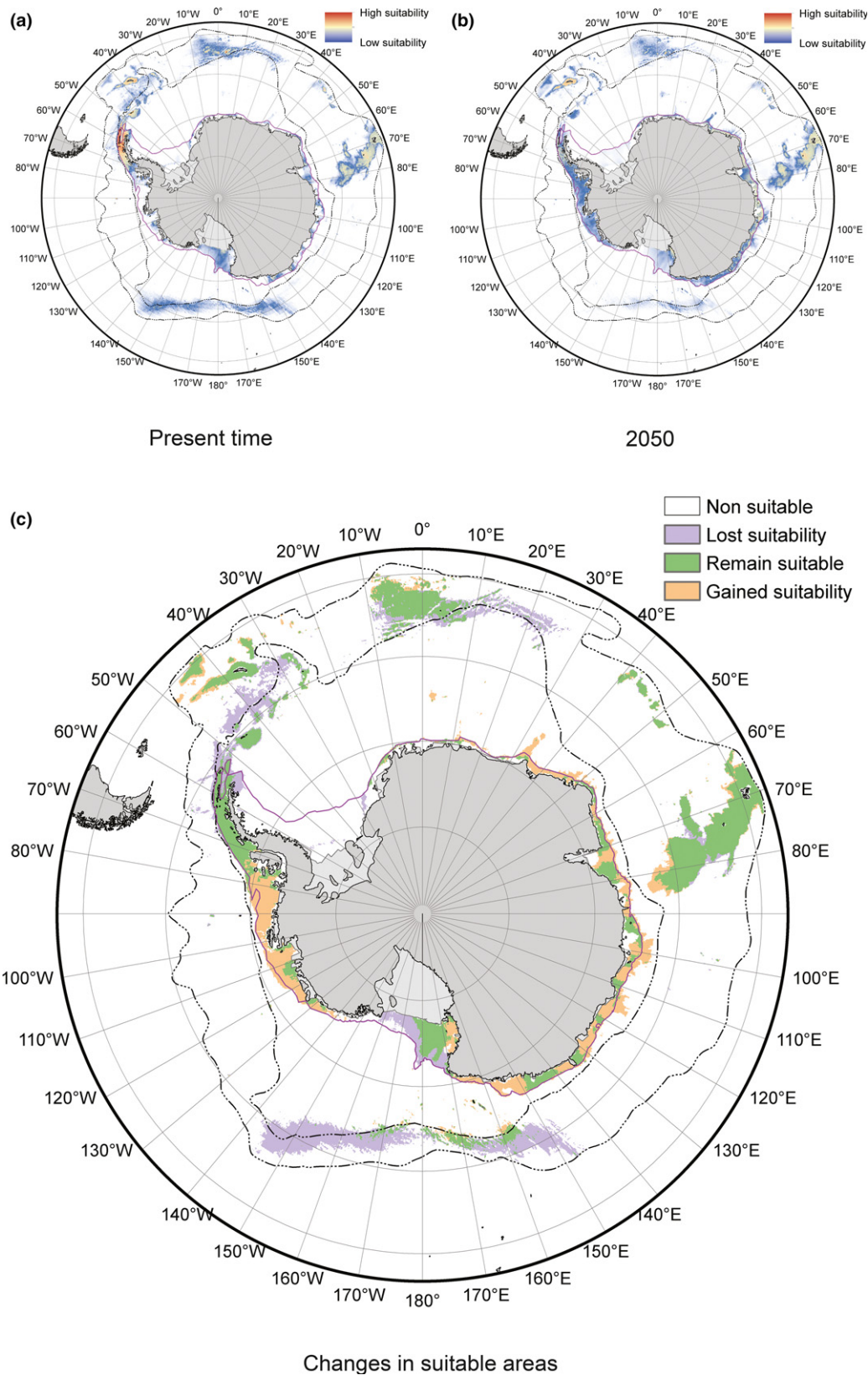
Figure 3 Species distribution model (SDM) generated with Maxent for *Bathylasma corolliforme* larvae. (a) Relative suitability on the Southern Ocean region for present conditions. Double dotted lines limit the Antarctic Circumpolar Current. (b) Relative suitability projected to the 2050 scenario. (c) Change in environmentally suitable areas for the year 2050. White areas remain unsuitable in present and future scenarios, green areas remain suitable and orange and purple areas denote transitions from non-suitable to suitable and vice versa.
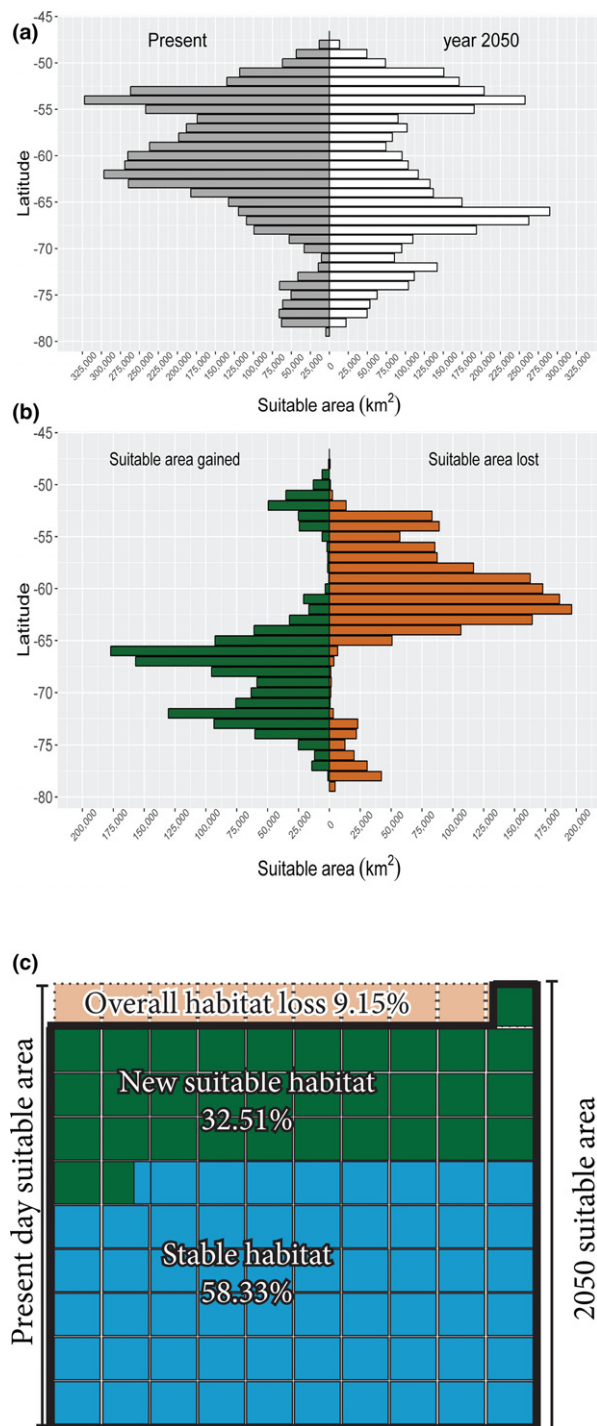
Figure 4 Total area found environmentally suitable for *Bathylasma corolliforme* larvae in the Southern Ocean. (a) Present and near-future (2050) scenario suitable area, plotted as function of latitude. (b) Total habitat gain (areas found environmentally unsuitable in the present scenario but suitable in the 2050 scenario) and habitat loss (from suitable to unsuitable). (c) Portrayal of the change in total suitable areas for *B. corolliforme* larvae, as percentage of the present scenario, showing total habitat loss and percentages of new and stable habitat.

offers protection for planktonic stages inhabiting the upper strata of the water column from ultraviolet radiation (Lister *et al.*, 2010). These two facts might explain the environmental preference described in the larval SDM: a trade-off between access to suitable food sources (ice-free areas) and environmental stability (sea-ice covered areas) resulting in higher suitability in areas covered by sea-ice during 20–30% of the year (see Fig. S4d).

The influence of bathymetry on the larval SDM might be in response to the distance to the source in the benthos – both models show response curves to depth changes of similar shape – although a bathymetric influence on larval communities in Antarctica has been acknowledged previously (Shreeve & Peck, 1995; Gallego *et al.*, 2014).

Consequences of altered habitat suitability

In response to changing climatic conditions, species frequently alter their geographic distributions, either showing latitudinal shifts, reductions/extensions in habitat suitability or extinction due to habitat loss (marine examples: Beaugrand *et al.*, 2002; Lindley & Batten, 2002; Thomas *et al.*, 2004; Brierley & Kingsford, 2009; Basher & Costello, 2016). In organisms with a biphasic life cycle, these distribution changes will result from a combination of the effects of climate change on both adults and larvae. For sedentary marine organisms such as barnacles, dispersing larvae are the sole stage in the life cycle that provides opportunities for species to mitigate the effects of climate change by altering their geographic distributions. Consequently, knowledge of the impacts of climate change on larval forms is critical for understanding the broader impacts on species distributions, and has been noted as one of the remaining challenges of modelling the geographic distributions of marine organisms (Dambach & Rödder, 2011). While a number of studies have considered the effects of climate change on the geographic ranges of benthic organisms, few have simultaneously considered the impact on their larval forms (Kirby *et al.*, 2007; Banks *et al.*, 2010; Byrne *et al.*, 2016), and none have adopted a SDM approach.

A key finding of our study is that the environmentally suitable areas for larvae and adults are spatially disjunct in the 2050 scenario; maximum suitability in the adult SDM occurs in the Bellingshausen Sea, the Antarctic Peninsula and the Scotia Arc, while the larval model predicts little environmental suitability in the waters connecting these islands and the Antarctic Peninsula. Furthermore, most habitat gain for adults occurs at low and high latitudes (Figs 2 & 4), while for larvae the habitat gain concentrates between 65° and 72° S.

How the predicted loss of environmental suitability and its latitudinal shift will affect extant populations of *B. corolliforme* is not yet clear, but one aspect likely to be altered is the extent of connectivity among benthic populations (Munday *et al.*, 2009). Reduced environmental suitability for

adults on the shelf break may result in habitat fragmentation, and consequently, larvae will need to travel longer distances through unsuitable waters to reach these habitats. Prolonged loss of environmental suitability over generations could compromise the persistence of some local populations, for example, in the Weddell and Ross Seas.

Significance and future directions

Our study addresses the effects of climate change on the geographic distribution of a benthic species, with consideration of the effects on both adult and larval stages. Modelling each life stage independently not only estimates potential ranges but also provides significant insights into how changes in the environment may affect the extent of environmentally suitable areas. Such changes will not necessarily operate equivalently for adults and larvae, and this mismatch would be overlooked if only one life stage were considered. Our study was possible because *B. corolliforme* larvae are easy to identify morphologically, which might reduce the transferability of this study to other benthic species. One way of augmenting the larval dataset to include other species might include the application of molecular identification techniques (namely metagenomics or metabarcoding) to plankton samples collected with the Continuous Plankton Recorder over vast areas from the world's oceans.

Our models suggest high sensitivity of larval stages to changes in sea-ice extension. A recent modelling study (Smith *et al.*, 2014) forecast a 56% decrease of summer sea-ice concentration in the Ross Sea by 2050 – in contrast with the predicted increase in sea-ice extension used in our model – and an associated greater dominance of diatoms in phytoplankton assemblages. Such a scenario might reduce the loss of environmentally suitable areas for the larval stages within the Ross Sea, but only by incorporating larval forms into global SDMs can we predict the impact of such changes on benthic meta-populations. Accordingly, we recommend that SDMs, in combination with genetic estimations of population connectivity and mechanistic models of dispersion, should be added to the set of tools employed to understand the population dynamics of benthic species and their responses to environmental changes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Data used in the construction of *Bathylasma corolliforme* SDMs.

Appendix S2 Literature sources used in the generation of the SDMs.

Appendix S3 Full description of the SDMs generated for *Bathylasma corolliforme*.

BIOSKETCH

Ramón Gallego is a marine ecologist focused in meroplankton studies, and especially in the combined application of species distribution models and molecular techniques on species identification and detection.

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