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Article type : Primary Research Article

Is the southern crab *Halicarcinus planatus* (Fabricius, 1775) the next invader of Antarctica?

Running title: Crab biological expansion into the Antarctic

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Funding information

FONDECYT Regular 1161358; INACh DG 14-17; Chilean national doctoral scholarship CONICYT 21151192; Fondap-IDEAL 15150003; PIA CONICYT ACT172065; FONDECYT 1160877; “Fonds pour la Formation à la Recherche dans l’Industrie et l’Agriculture” (FRIA); “Bourse Fondation de la Mer”; Contribution Nº23 to the “Refugia and Ecosystem Tolerance in the Southern Ocean” project (RECTO; BR/154/A1/RECTO) funded by the Belgian Science Policy Office (BELSPO); IPEV program Nº1044 Proteker; Contribution Nº48 to the vERSO project (BELSPO, contract n°BR/132/A1/vERSO).

Abstract

The potential for biological colonisation of Antarctic shores is an increasingly important topic in the context of anthropogenic warming. Successful Antarctic invasions until now have been recorded exclusively from terrestrial habitats. While non-native marine species such as crabs, mussels and tunicates have already been reported from Antarctic coasts, none have as yet established there. Among the potential marine invaders of

Antarctic shallow waters is *Halicarcinus planatus* (Fabricius, 1775), a crab with a circum-Subantarctic distribution and substantial larval dispersal capacity. An ovigerous female of this species was found in shallow waters of Deception Island, South Shetland Islands in 2010. A combination of physiological experiments and ecological modelling was used to assess the potential niche of *H. planatus* and estimate its future southward boundaries under climate change scenarios. We show that *H. planatus* has a minimum thermal limit of 1 °C, and that its current distribution (assessed by sampling and niche modelling) is physiologically restricted to the Subantarctic region. While this species is presently unable to survive in Antarctica, future warming under both strong mitigation' and 'no mitigation' greenhouse gas emissions scenarios will favour its niche expansion to the Western Antarctic Peninsula (WAP) by 2100. Future human activity also has potential to increase the probability of anthropogenic translocation of this species into Antarctic ecosystems.

Keywords (6-10): Niche modelling, Southern Ocean, climate change, thermotolerance, survival, establishment, reptant crab, non-native species.

Introduction

Biological invasions are an important component of global change, and one of the most critical global threats to native biodiversity (Sax et al., 2005). According to Richardson et al. (2000), a non-native species becomes an invasive species when a set of individuals is able to traverse natural barriers (whether geographic, environmental, or ecological) and subsequently establish in new habitats. While numerous anthropogenic activities can promote invasions, climate change may represent a particularly potent threat to natural ecosystems (Malcolm et al., 2006). Both the rate and dimension of biological invasions are likely to be influenced by global warming (Walther et al., 2009). Understanding the mechanisms and routes of such range shifts or species introductions may help facilitate the design of strategies for controlling or preventing invasion (Estoup & Guillemaud, 2010).

Notwithstanding the wide expanse of Southern Ocean waters isolating the southern tip of South America from other land masses, several non-native species have been reported in the Antarctic over recent decades (Smith & Richardson, 2011). These examples include the invasive grass *Poa annua* (Chwedorzewska et al., 2015; Molina-Montenegro et al., 2012), seeds of the toad rush *Juncus bufonius* (Cuba-Díaz et al., 2013), the invasive mosquito *Trichocera maculipennis* (Potocka & Krzemińska, 2018), and several South American invertebrates (e.g. insects, worms, freshwater crustaceans; Hughes & Worland, 2010). Non-native species have also been reported in marine habitats and in the shallow subtidal zone, in particular in the South Shetland Islands (e.g. decapods and bivalves) and East Antarctica (i.e. bryozoans, hydrozoans, and tunicates) (Avila et al., 2020; Cárdenas et al., 2020; McCarthy et al., 2019). However, there is as yet no evidence for any non-native marine species having established in Antarctica.

Reaching Antarctic coasts requires dispersal across vast and deep biogeographic barriers that have isolated the continent for millions of years, including traversal of the westward flowing Antarctic Circumpolar Current (ACC) that apparently impedes latitudinal dispersal (Clarke et al., 2005; Rintoul, 2009). The extreme cold temperatures of Antarctic waters (<+2 °C) also imply a strong ecophysiological constraint to the survival and development of non-native marine species that have not adapted to near-zero and subzero temperatures (Fraser et al., 2007; Marsh et al., 2001; Peck, 2016) that can reach down to -1.85 °C in winter. Consequently, Antarctic marine communities have been considered among the most isolated and endemic on Earth and invasion by non-native species as unlikely (Clarke et al., 2005; Griffiths et al., 2009).

Human activities such as fisheries, tourism and scientific operations rely on direct maritime traffic between Antarctica and lower latitude coasts, including potential transport of non-native organisms through ship hull fouling and larval propagules via ballast water (Lewis et al., 2003; Lewis et al., 2005). With more than 50,000 tourists visiting the same west Antarctic spots each southern summer (McCarthy et al., 2019), and 4,000 scientists working in Antarctica during the summer and 1000 in winter (Hughes & Convey, 2014), tourism and science represent the main vectors of Subantarctic propagule pressure on Antarctic communities (Avila et al., 2020; Diez & Lovrich, 2010; Galera et al., 2018; Hellmann et al., 2008; Lee & Chown, 2007; Meredith & King, 2005; Tavares & De Melo, 2004). Consequently, records of non-native species in Antarctica are increasing in number, with potential for establishment now primarily constrained by ecological and physiological limitations. As the climate continues to warm, the potential for successful marine invasions into Antarctica is projected to increase substantially (Galera et al., 2018; Hellmann et al., 2008; Richardson et al., 2000).

The West Antarctic Peninsula (WAP) is the Antarctic region where the strongest climate warming has been recorded in the continent over the last 50 years (Convey et al., 2009; Gutt et al., 2015; Turner et al., 2014). Seawater and air temperatures have increased by +1 ºC and +7 °C, respectively, in the past half-century (Meredith & King, 2005; Schram et al., 2015), with particularly pronounced increases in winter air temperatures (King et al., 2003; Vaughan et al., 2003) and corresponding reductions in sea ice cover (Ducklow et al., 2013; Schofield et al., 2017; Stammerjohn et al., 2012; Turner et al., 2016). Global climate change may cause typically sub-zero Antarctic waters to warm up to (and beyond) zero, potentially providing suitable conditions for the survival of non-native species along Antarctic coasts (Galera et al., 2018; Hellmann et al., 2008).

In February, 2010 an ovigerous female of *Halicarcinus planatus* (Fabricius, 1775) (Brachyura, Hymenosomatidae) was found alive in shallow subtidal water of Deception Island (WAP; Aronson et al., 2015). Previous to this record, Stebbings (1914) reported this species in Macdougal Bay, South Orkney Islands, however the reliability of this occurrence has been questioned, considering its circum-Subantarctic distribution (Yaldwyn, 1965; Thatje & Arntz, 2004; Diez & Lovrich, 2010; Aronson et al., 2015). *Halicarcinus planatus* is the only hymenosomatid crab that inhabits shallow waters (Garth, 1958; Varisco et al., 2016) of southern South America and the Subantarctic Falkland/Malvinas, Marion, Crozet, Kerguelen and Macquarie islands (Aronson et al., 2015; Boschi et al., 1969; Griffiths et al., 2013; Melrose, 1975; Richer De Forges, 1977). This small crab (carapace width up to 15 mm and 20 mm for female and male, respectively, in Punta Arenas; Fig. 1) is an opportunistic feeder (Boschi et al., 1969) commonly found sheltered under rocks in the intertidal and subtidal zones, in between holdfasts of the giant kelp *Macrocystis pyrifera* or sheltered in hydrozoans and mussel colonies (Chuang & Ng, 1994; Richer De Forges, 1977; Vinuesa & Ferrari, 2008).

The potential of marine taxa to establish in Antarctic waters is likely heavily constrained by ecological and physiological adaptations. *H. planatus* has a strong dispersal potential mediated by an extended planktonic larval stage (Diez & Lovrich, 2010; Ferrari et al., 2011; Richer De Forges, 1977) lasting between 45 and 60 days (at temperatures of 11-13 °C and 8 °C, respectively, in the laboratory) prior to benthic settlement (Boschi et al., 1969; Diez & Lovrich, 2010). This species has the physiological capacity to withstand low temperatures. Most decapod taxa exposed to cold waters experience increased magnesium ion concentration in the hemolymph ($[Mg^{2+}]_{HL}$), reducing metabolic rate and aerobic activity, potentially leading to death (Aronson et al., 2007; Diez & Lovrich, 2010; Frederich et al., 2001; Thatje et al., 2005). However, *H. planatus* has the capacity to overcome these issues by reducing $[Mg^{2+}]_{HL}$ (Frederich et al., 2001), providing capacity for survival in cold waters like the Kerguelen Islands, where winter seawater temperatures range between +1.1 and +3.0 °C (Féral et al., 2019). A broad analysis Diez & Lovrich (2010) considering its broad Subantarctic distribution, high dispersal potential and ability to live at low temperatures concluded that *H. planatus* is the most likely future decapod invader of Antarctic shallow waters.

Following the recent discovery of a living specimen of *H. planatus* in Deception Island, we evaluate in this study the capacity of the species to settle and spread in the WAP and adjacent islands by combining experimental design and a niche modelling approach. Correlative niche modelling approaches have long proved useful to project the distribution range of species for conservation purposes under stable environmental conditions (Richardson & Whittaker, 2010). However, in the context of climate change, ecophysiological data are required to assess the capacity of organisms to survive under changing environmental conditions. In this study we assessed experimentally the physiological capacity of *H. planatus* to tolerate extreme cold conditions in the laboratory, and we evaluated the probability of the species to expand its distribution range southward using a Species Distribution Model (SDM). The modelled distribution of *H. planatus* was first projected under current climatic conditions to evaluate its distribution range in Subantarctic and Antarctic regions. Then the species distribution was modelled under the 'strong mitigation' and 'no mitigation' scenarios (RCP 2.6 and RCP 8.5, respectively) for 2050 and 2100 to determine the probability that *H. planatus* will colonize Antarctic shallow water habitats in the future. RCP scenarios assess the evolution of the atmospheric radiative forcing towards 2300, and correspond to the level of the projected radiative forcing in 2100, expressed in W/m^2 (RCP 2.6 corresponds to $2.6W/m^2$ in 2100; https://sos.noaa.gov/datasets/catalog/datasets/air?ordering=name).

Material and methods

Experimental design

Ethical Protocol

All experiments were performed in compliance with bioethics guidelines established by the *Comisión Nacional de Ciencia y Tecnología de Chile* (CONICYT) and the CICUA of the Universidad de Chile (*Comité Institucional de Cuidado y Uso de Animales*).

Thermotolerance experiments

One hundred and twenty adult individuals of *H. planatus* were collected alive in the subtidal zone by SCUBA diving at *Rinconada Bulnes* (RB) (53°35'49.91"S, 70°56'5.19"W, south of Punta Arenas, Chile) on April 9, 2018. Individuals were transported to the IDEAL-CENTER laboratory (Punta Arenas) and distributed into 6 containers for the experiment. In each container (Appendix 1) 15 females and 5 males were isolated individually in 1 dm^3 glass jars of seawater containing a 2 cm-long PVC tube (2.5 cm diameter). This unequal sample size between gender reflected to the disproportional sex ratio in nature (Diez et al., 2011; Vinuesa & Ferrari, 2008); at the time of collection, 30% of the crabs were males and 70% were females. A plastic container of seawater was used for water replacement. Each jar and container were aerated and temperature was controlled by a cooler exchanger (Alpha RA12 and RA8, Lauda-Koenigshofen®, Germany). Individuals were acclimated for 15 days with temperature, salinity and photoperiod adjusted to the sampling location (9 °C, 30 PSU, 11hrs light/13hrs dark on April 9, 2018). Individuals were fed every 4 days with thawed and chopped mussels and polychaetes. The next day, 30% of seawater was removed from each jar, sucking the bottom to eliminate faeces and food debris. Recipients were then refilled with clean seawater at the exact same temperature and salinity from the plastic seawater container. The latter was then refilled with new seawater, which had time to reach the specific temperature before the next refill. After acclimation, temperature was reduced by 0.5 °C every day until it reached a threshold value set at 5 °C (control; minimal seawater temperature in Punta Arenas), 2 °C, 1 °C, 0 °C, -1 °C or -1.8 °C, depending on the experiment, which was conducted for 90 days following (Vargas-Chacoff et al., 2009). The different temperature threshold values used in the experiment correspond to subtidal temperatures recorded in Fildes Bay (62°12'11.95"S 58°56'37.00"W; King George Island, South Shetland Islands, WAP) which ranged between -1.9 ºC and 2.1 ºC; summer average 1.2 ºC (-0.2 ºC to 2.1 ºC) and winter average -1.6 ºC (-1.9 ºC to -1.1 ºC) in 2017 (data from IDEAL-CENTER, published by Cárdenas et al. (2020). The 90 days simulate the duration of winter. Survival was checked each morning, and dead specimens were removed and preserved in 96% ethanol.

Salinity and larval experiments

To assess survival at different salinities, adult individuals of *H. planatus* were collected at the same location (RB) on July 5, 2018, transported to the laboratory and separated in containers. Eighteen females and 4 males were isolated in recipients of 10 dm^3 filled with seawater. After a 15-day acclimation period at the same temperature, salinity and photoperiod as the sampling location (5 °C, 30 PSU, 8:16 L:D), individuals were submitted to different salinities of 30 PSU (control 1), 23 PSU, 18 PSU, 11 PSU and 5 PSU for 39 days at 5 ºC. In parallel, some individuals submitted to natural 18-PSU seawater collected in Skyring Sound (52°33'48.07"S, 71°34'15.54"W) were used as a second control. The previously detailed protocol for feeding and cleaning was followed. Survival was checked every morning and dead specimens were removed and preserved in 96% ethanol.

During the salinity experiment, at 30 PSU some individuals released larvae which were subsequently collected and placed in 1 dm^3 glass jars (200 larvae in each) filled with seawater at 5 ºC, 2 ºC and 1 ºC for 12 days. Crab larvae were fed daily with newly hatched nauplii. Their survival was checked on days 1, 3, 6, 8, 10 and 12 and on the cleaning day which consists of complete seawater replacement. Dead individuals were removed and preserved in 96% ethanol.

Species distribution modelling

Species Distribution Models (SDM) are used to project the distribution of organisms based on the statistical analysis of spatial relationships between environmental conditions and species records (Elith et al., 2006; Peterson, 2003; Peterson et al., 2011). SDMs have been widely used in past decades in various applications, including assessing species potential distribution (Guillaumot et al., 2018; Nachtsheim et al., 2017; Reiss et al., 2011) and evaluating potential changes in projected suitable areas under environmental shifts (Berry et al., 2002; Engler et al., 2009; Meier et al., 2011; Pearson & Dawson, 2003; Thomas et al., 2004).

Occurrence dataset

The study had a limited geographic extent where occurrence records have been reported (Longitude: 70.5°E to 75.5°W, Latitude: 36°S to 70.5°S). Presence and absence data were collected during different sampling expeditions carried out between 2015 and 2019 (PROTEKER 1, 4, 5 and 6, INACH ECA 53, 54 and 55), obtained from collaborators and retrieved from IOBIS and GBIF databases and from the scientific literature (Appendix 2). The georeferencing of each occurrence was verified and for this study; repeated geographical points were removed. The identification of collected specimens was checked following current taxonomy

(Boschi, 1964). Occurrences located north of 34°S in Chile were not considered, since these points were outside the distribution range of the species and could not be corroborated.

A DarwinCore-compliant dataset was built using presence and absence data of *H. planatus* occurring on Subantarctic islands and South America between 1948 and 2019. Four types of records were included: individualized by specimen, by groups, records obtained from bibliographic reviews and absence records. The dataset is published in GBIF (GBIF, 2018; Lopez et al. 2020).

Distribution models were built using 314 presence records of both adults and larvae, and 57 absence records (Fig. 2, Appendix 2).

Environmental datasets

The distribution of *H. planatus* was modelled using 16 available environmental parameters as descriptors of the crab habitat (Table 1). Depth and its derivatives (slope and roughness) were taken from GEBCO (Table 1). Other descriptors were compiled from the Bio-Oracle Marine layers dataset and obtained from pre-processed global ocean re-analyses, combining satellite and *in situ* observations in regular two- and three-dimensional spatial grids (Assis et al., 2018). Minimal, maximal and mean values were used as descriptors and combined as suggested in the literature (Bucklin et al., 2015; Franklin, 2010). Environmental layers provide average monthly values for the present decade [2000-2014] at a spatial resolution of 5 arc-minutes (about 8 x 8 km) and describe monthly averages for the period 2000-2014.

Species distribution was also modelled according to two greenhouse gas emissions scenarios, RCP 2.6 and RCP 8.5 scenarios for future decades 2040-2050 and 2090-2100 (IPCC, 2013). Maps of projected changes in ocean conditions were downloaded from Bio-Oracle (https://www.bio-oracle.org/index.php; Table 1). The RCP 2.6 scenario (Appendix 3) projects an increase of mean seafloor temperatures of up to +0.7 °C along the Argentinian coast by 2100, +1.3 °C in the Weddell Sea region and +1.3 °C on the northern Kerguelen Plateau. Salinity is projected to be less than RCP 8.5, along with a decrease in ice thickness with maximal depletion values of -30 cm in the south of the WAP by 2100. The RCP 8.5 scenario (Appendix 3) for decade 2040-2050 projects that seafloor waters will warm by +1 °C along the southern South American coasts and in the Weddell Sea, and for decade 2090-2100 projects an increase of seafloor mean temperatures of up to +4 °C along the Argentinian coasts, +0.5 to +1 °C in the WAP, up to +3 °C on the northern Kerguelen Plateau and a projected decrease of -0.5 to -1 °C in insular regions such as South Georgia and the South Orkney Islands. Salinity is projected to decrease in the Subantarctic and Antarctic regions by -0.1 to -0.2 PSU unit for the 2050 and 2100 scenarios, respectively, with close tendencies between RCP 2.6 and RCP 8.5. Sea ice thickness is projected to reduce in some areas from a few centimetres to 0.6 m in RCP 2.6 scenario and up to 1.2 m for RCP 8.5 scenario, resulting in an expansion of ice-free areas in the Weddell Sea region (Fig. S3.1).

Primary production and oceanographic current speed for decades 2040-2050 and 2090-2100 were considered unchanged and similar to present-day conditions.

In order to spot and remove extrapolation errors, the Multivariate Similarity Environmental Estimate (MESS; Elith et al., 2010) was computed based on presence records (Guillaumot et al., 2019; Guillaumot et al., 2020). The MESS provides an estimate of the range of environmental conditions under which species occurrences were found and used to calibrate the model. It is then used to select areas where model projections will be calculated, dismissing areas where environmental conditions are not met, and where the model extrapolates. This was helpful to prevent from projecting the model far from the conditions in which the species can be found (noteworthy for depth).

Model calibration

Species distribution models were generated using the Boosted Regression Trees (BRT) algorithm with the following settings; learning rate 0.005; bag fraction 0.9 and tree complexity 4. These settings minimise the model projective deviance according to the tests generated following Elith et al. (2008) (Appendix 4). The R package 'gbm' was used to run the model (Elith et al., 2008; Ridgeway, 2006). Models were calibrated using presence and absence data. Modelling performance was assessed using a spatial random cross-validation procedure adapted from Guillaumot et al. (2019), using absence records for model calibration (instead of background records). Also, considering the limited number of occurrence records available and their patchy distribution at a broad spatial scale, the occurrence dataset was randomly split into 5 spatial parts, with 80% of the dataset used as a training subset and 20% used as a test subset (Elith et al., 2008). The procedure was repeated 20 times to generate a set of 100 model replicates. The proportions of presence and absence data falling into areas projected as suitable and unsuitable for the species distribution were evaluated to assess model performance. Model performance was also assessed using the Area Under the Curve (AUC; Fielding & Bell, 1997), the True Skill Statistics (TSS; Allouche et al., 2006) and the Biserial Correlation metrics (COR; Elith et al., 2006).

Model outputs

Model projections were projected on the entire study area (Longitude -76°E, 178°W, Latitude -35°S, -68°S) with a focus mainly on areas where the species is reported presently and where it may be expected in the future, in southern South America, the Scotia Arc and the WAP, the WAP alone and the Kerguelen Plateau.

Results

Survival rate in the temperature experiment

One individual died the next day after reaching the target temperature in the -1.8 °C temperature experiment. Survival rate at -1.8 °C reached 0% on day 11. Survival reached 0% on day 15 at -1.0 ºC. Survival rate at 0 ºC was 52% on day 27 and 0% on day 59. Survival rates were 60% at 1 °C, 75% at 2 °C and 95% at 5 °C on day 90. (Fig. 3).

Survival rate of adults and larvae in the salinity experiment

Survival rate in the salinity experiment at 5 PSU was 0% on day 2. Survival rate at 11 PSU was 0% on day 14. Survival rate was 50% on day 36 and 36% on day 39 at 18 PSU. Interestingly, survival rate was over 50% (67%) for the experiment at 18 PSU performed with seawater from Skyring Sound. Survival rates were 95% on day 39 at 25 PSU and 30 PSU (Fig. 4).

Females collected on July 5 were ovigerous and released larvae at the end of August at 5 ºC, 30 PSU and 25 PSU. The survival rate of larvae at 1 ºC was 62.5% on day 12. Survival rates at 2 ºC and 5 ºC were 85% and 92.5%, respectively, on day 12 (Fig. 5).

SDM projections under current environmental conditions [2000-2014]

SDMs showed very high AUC scores of 0.947 ± 0.059, TSS of 0.795 ± 0.123 and biserial correlation COR of 0.873 ± 0.070. Correctly classified test data also reached high scores (89.9 ± 0.3% for presence test records and 92.9 ± 2.2% for absence test records correctly classified). The proportion of areas where the model extrapolates was very high (86.3%, Fig. 7), highlighting again the relevance of using the MESS method as recommended by Guillaumot et al. (2019, 2020).

Mean sea ice thickness (40.1 ± 3.2%) and seafloor temperatures are the two main drivers of the species distribution (mean, maximal, and minimal seafloor temperatures with 37.8 ± 3.7, 7.6 ± 1.9 and 6.9 ± 2.4% contribution to the model, respectively, Table 2), with suitable areas corresponding to low sea ice cover (<0.1%) and minimum temperatures over +2 °C (Fig. 6). These environmental values match perfectly with the latitudinal partition in the distribution of *H. planatus*, with warmer temperatures (>+2 °C) and lower ice coverage (<0.1%) at the lower latitudes associated with most presence records and few absences, and in contrast, colder temperatures (<+2 °C) and thicker sea ice coverage (>0.1%) associated with the single presence reported in the WAP and most absence records. Interestingly, primary production is not a good projector of the species' distribution (<1%).

As occurrence records are mainly distributed in coastal shallow water areas, depth does not contribute much to the model as no contrast in bathymetry values are present in the dataset. Slope and roughness have probably more contrasting values in deep-sea habitats and consequently do not contribute significantly to the model (<0.2%).

The extrapolation mask importantly reduced the area projected to shallow habitats (Fig. 7). Distribution probabilities projected by the model were highest in southern South America, New Zealand and Australia and most Subantarctic islands (Kerguelen, Heard, Marion, Bouvet and South Sandwich Islands; Fig. 7A). Interestingly, the model projects an intermediate probability of distribution in South Georgia, for which a single absence was reported (Fig. 2), and a high probability on Heard Island, where no occurrence data has been reported yet. The WAP is projected as unsuitable to the survival of *H. planatus*, as in the case of Deception Island (Fig. 7C).

SDM projections under future environmental conditions

SDM future projections under RCP 2.6 in decades 2040-2050 and 2090-2100 project respectively low and intermediate probability of *H. planatus* to settle in South Georgia, Elephant Island and the WAP, (Fig. 8, 9). The RCP 8.5 scenario showed an increase in probability for *H. planatus* to survive in the WAP (Fig. 10, 11). Models project higher presence probabilities compared to present-day projections in South Georgia and the South Shetland Islands for both decades 2040-2050 and 2090-2100, with the highest values projected in the northern tip of the South Shetland Islands. The South Orkneys are not projected as suitable by 2040-2050, but some patches of suitable areas appear by 2090-2100.

Discussion

This study combines physiological and ecological modelling approaches to highlight the increased risk of marine incursions into Antarctic coastal ecosystems over the coming century. Specifically, we reveal that the widespread Subantarctic decapod *H. planatus* has significant potential to establish in Antarctic waters under realistic climate change scenarios in the coming decades. More broadly, this prospect of future marine introductions into Antarctic ecosystems potentially has crucial implications for the conservation of endemic Antarctic coastal assemblages. Indeed, over recent decades an increasing number of non-native marine taxa have been reported from Antarctic ecosystems, including: *Rochinia gracilipes* in the South Shetland Islands (Griffiths et al., 2013); *Bugula neritina* (Bryozoa) off Dronning Maud Land (East Antarctica) in the 1960s (McCarthy et al., 2019); *Hyas araneus* (Decapoda) from Elephant Island in the 1980s (McCarthy et al., 2019); *Ectopleura crocea* (Hydrozoa) and *Ciona intestinalis* (Ascidiacea) off Dronning Maud Land and off Queen Mary Land (East Antarctica) in the 1990s (McCarthy et al., 2019). Newer records since 2000 include *Emerita sp.* and *Pinnotheres sp.* (larval stage) in King George Islands in the 2000s (Thatje & Fuentes, 2003); *H. planatus* from Deception Island (Aronson et al., 2015); *Membranipora membranacea* (Bryozoa) and *Macrocystis pyrifera* (brown algae) from Deception Island (Avila et al., 2020); *Durvillaea antarctica* (brown alga) from King George Island (Fraser et al., 2018) and Livingston Island (Avila et al., 2020); and *Mytilus* cf. *platensis* (Bivalvia) in King George Island (Cárdenas et al., 2020) in the 2010s.

There are potentially several different modes of dispersal for species to reach Antarctica. Fraser et al. (2018) and Avila et al. (2020) identified dispersal by rafting on buoyant kelps as a possible mechanism for the arrival of non-native species to Antarctica. The former study also included a Lagrangian analysis to show that particles released from South Georgia and the Kerguelen Islands were able to drift across the Polar Front and reach Antarctic coasts following strong storm events. According to this model, storm conditions may enable buoyant kelps to reach the WAP. Such conditions may not be rare, as remains of the kelp *D. antarctica* were observed onshore in the WAP in 2019 and 2020 (López-Farrán, personal observation). Direct observations (from southern New Zealand) of adult *Halicarcinus planatus* individuals associated with *D. antarctica* holdfasts, and also in detached, drifting *D. antarctica* at sea (Waters, unpublished data) imply rafting as a direct mechanism for adults of this decapod taxon into Antarctic waters. Anthropogenic activities may also be potential dispersal vectors for this decapod (Avila et al., 2020; Cárdenas et al., 2020) (e.g. via ship hulls, ballast waters, outdoor and personal equipment of tourists or oceanographic equipment of scientists).

No established non-native marine species have as yet been observed in Antarctica, suggesting that physiological barriers may be key in preventing such invasions (Richardson et al., 2000). In this study, we combined two independent approaches to define the environmental and geographical boundaries of *H. planatus* distribution under present and future environmental conditions. SDM provides an estimate of a species' 'realised niche' (Hutchinson, 1957; Soberón, 2005, 2010). The thermal limit of *H. planatus* established experimentally in this study corresponds to the coldest conditions of its Subantarctic distribution, located in the

Kerguelen Islands, where subtidal temperature ranges between +1.1 and +3.0 °C during the Austral winter (Féral et al., 2019; Lucas, 1980; Richer De Forges, 1977). This species can therefore potentially endure summer conditions in WAP (1 ºC and above) in a wide range of salinity (between 18 PSU and 30-33 PSU), but would not survive during the cold winter months. Our experimental results may indicate that Antarctic seawater temperatures may impede larval development even during the summer, suggesting that this species is not able to complete its development in Antarctica under present conditions. In parallel, the survival rates among larvae were 65%, 85% and 92% at 1, 2 and 5°C respectively, thus coinciding with adult rates, and confirming the sensibility to low temperature mentioned by Pörtner and Farrel (2008), confirming that at that stage larvae and adults can survive during Antarctic summer only.

Halicarcinus planatus has previously been highlighted as a potential invader of Antarctica (Diez & Lovrich, 2010), because of its potential to live in cold waters, through regulation of $[Mg^{2+}]_{HL}$. However, the present results demonstrated that this physiological characteristic is not sufficient to survive the sub-zero temperatures that typify current Antarctic winters (Fig. 3). The finding that brachyuran crabs cannot currently establish in Antarctica may also help to explain their extinction from shallow Antarctic habitats from the mid-Miocene, ~14 million years ago, when ACC intensification led to cooling and the establishment of a perennial sea-ice cover in the region (Crampton et al., 2016; Hansen et al., 2013; Thatje et al., 2005; Zachos et al., 2008). Numerous marine lineages including brachyurans, lobsters and sharks disappeared from Antarctic waters, along with most teleosteans except for cold-adapted nototheniids and liparids (Aronson & Blake, 2001; Aronson et al., 2007; Clarke et al., 2004). The simultaneous extinction of these diverse taxa was presumably driven by their lack of physiological tolerance to cold conditions (Aronson et al., 2007; Clarke et al., 2004; Frederich et al., 2001). Together, these data may highlight the crucial role of thermal barriers in preserving the integrity of Antarctic coastal ecosystem.

Physiological barriers to Antarctic incursions are projected to weaken under future warming scenarios with increased seawater temperatures and shortened sea-ice seasons. For example, near Palmer Station the ice season decreased by 92 days from 1979/80 to 2012/13 (Ducklow et al., 2013; Meredith & King, 2005). According to IPCC RCP scenarios the WAP will continue to warm (Appendix 3), facilitating the establishment of non-native species already arriving. *Halicarcinus planatus* is not able to establish in the WAP under present conditions because it is not a suitable environment (Table 2, Fig. 6, 7), however this may change in the future. In the South Shetland Islands, the worst scenario RCP 8.5 projects a decrease in ice thickness, the expansion of ice-free areas (Appendix 3) and a 1 to 2 °C increase of seafloor temperature in 2100, leading to suitable conditions for *H. planatus* establishment. SDM projections indicate the highest suitability for *H. planatus* presence in South Georgia and some places of the WAP (Fig. 11 B and C). The most optimistic climate change scenario RCP 2.6 projects a rise of seafloor water temperature of 0.4 ºC in the South Shetland Islands in 2100, resulting in intermediate SDM projections in the WAP and South Georgia (Fig. 9 B and C). Thus, according to these future scenarios it is just a matter of time before the WAP would reach suitable environmental conditions for *H. planatus*.

Survival is not the only requirement for the establishment of a species in a new area. A successful colonisation also implies developing, reproducing and then dispersing to new places (Richardson, 2000 modified), and active behaviour to escape, feed and mate (Frederich et al., 2001). According to SDM projections and the thermotolerance experiment, a successful colonisation would be possible in an environment at +2 ºC. Deception Island is the most active volcanic island of the South Shetland Islands, where many subtidal hydrothermal points and geothermal activity offer temperatures that could favour the establishment of non-native species (Agusto et al., 2004), converting Port Foster into a key location for their colonisation (Aronson et al., 2015; Avila et al., 2020). We searched for *H. planatus* in several places in the WAP during three SCUBA diving campaigns between 2017 and 2019, including where it was collected in 2010 - shallow waters off Baily Head outside the caldera of Deception Island (Aronson et al., 2015) - and other active sites (within the caldera of Deception Island, in Penguin Island (South Shetland Islands), and Paulet Island in the Weddell Sea), or inactive sites like King George Island (South Shetland Islands), Doumer Island, Roberts Island, Coppermine Peninsula, Chile Bay in Greenwich Island, among other places, and none were found. This absence agrees with our results, but contradicts the presence of the ovigerous female in Deception Island (Aronson et al., 2015), which would need at least two years to reach pubertal moult, the time required in the Kerguelen Islands (Richer De Forges, 1977). This female certainly would not have grown up *in situ*; this place is on the outer coast under full Antarctic conditions (without geothermal activity or hydrothermal influence typical of the interior of Deception Island). Our results suggest its arrival at the mature stage or maybe the ovigerous stage, implying that its development was completed elsewhere. An arrival through rafting is also unlikely. Early stages of *H. planatus* have been observed in floating kelps (*Macrocystis pyrifera*) in the Internal Sea of Chiloé (Hinojosa et al., 2010), and kelps have been reported in Deception Island (Avila et al., 2020). However, the journey from the Subantarctic area to the WAP implies two years across the SO riding kelps, which is highly improbable. This female was more probably brought through the Drake Passage by ship during the southern 2009-2010 summer; the extraction of an adult crab together with kelps frond and holdfast wrapped around an anchor is quite likely (K. G. pers. obs.).

The establishment of non-native marine species in Antarctica is an issue that is becoming more pressing. The composition of the community may change dramatically according to which species establishes. Antarctica is characterized by the absence of durophagous predators (bony and cartilaginous fishes and brachyurans) on the continental shelf, and short food webs. The effects of the arrival of reptant crabs in the shallow Antarctic community were discussed from different points of view, either as a threat, taking the invasion of the red king crab *Paralithodes camtschaticus* in the Barents Sea for example (Aronson et al. 2007), or as a native component considering the distribution of the deep-sea lithodid on the continental slope (Griffith et al. 2013). *Halicarcinus planatus* is not yet established in Antarctica. Its small size, opportunistic feeding behaviour and soft exoskeleton definitely do not make it a top predator (Boschi et al., 1969). It feeds on phytoplankton remains accumulated at the bottom, such as carrion, detritus, mucopolysaccharides from algae and small soft individuals, even of its own species (López-Farrán, personal lab observation). They are prey for fishes (as *Harpagifer bispinis*, *Patagonotothen tessellata* and *Austrolycus depressiceps*; Fernández et al. 2010; Diez et al., 2011), birds, crabs and sea stars, among others, and look for refuge among rocks and kelp holdfasts to survive (Chuang & Ng, 1994; Richer De Forges, 1977; Vinuesa & Ferrari, 2008). *Halicarcinus planatus* is thus playing a fairly important role in food webs and is part of the Subantarctic ecosystem (Diez et al., 2011; Richer De Forges, 1977). However, as it is not considered as a keystone or a bioengineer species, the establishment of this crab would not affect the Antarctic ecological community significantly. Although the effects of non-native species are impossible to project, *H. planatus* may just incorporate into the already well-represented detrivorous guild of the WAP shallow benthic ecosystems. Under warmer conditions (2 °C), the increase of seawater temperature would affect the WAP ecosystem much more intensively than the arrival of a small soft-shelled detritivorous brachyuran such as *H. planatus* (Ashton et al., 2017; Clark et al., 2019; Griffiths et al., 2017; Turner et al., 2014). An example of a bioengineer species that would impact the intertidal and shallow subtidal in the WAP is *Mytilus* cf. *platensis*, a non-native species recorded in 2019 (Cárdenas et al., 2020). Mussels have the capacity to provide dense three-dimensional matrices (Alvarado & Castilla, 1996) that persist for long periods, constituting a micro-habitat which reduces desiccation during low tides, offering a stress-free space for small fish, invertebrate and alga species (Prado & Castilla, 2006).

Antarctic water temperature continues to rise and stirs up the debate on the potential establishment of incoming species through transport on ship hulls, in ballast waters or on floating kelps (Aronson et al., 2015; Avila et al., 2020). Maritime traffic and tourism have increased the footprint and intensity of human activity in Antarctica (Kruczek et al., 2018, Hughes et al. 2019), raising the pressure of propagules in marine Antarctica, and this will probably continue to increase in the next years (Kruczek et al., 2018). However, the involuntary introduction of non-native species to the Antarctic region and the movement of species and/or individuals within Antarctica from one zone to any other are among the highest priority issues considered for the Committee for Environmental Protection (CEP) and the Scientific Committee for Antarctic Research (SCAR). Therefore, a strong effort has been invested to improve the ballast water management of ships in Antarctica and to develop a strategy for biofouling (MEPC, 2011).

Regardless of whether *H. planatus* individuals are able to reach the WAP by themselves or not, the SDM projected under conditions of IPCC RCP 2.6 or 8.5 climate scenarios indicate that individuals could survive and settle, either sooner (Fig. 8 and 9) or later (Fig. 10 and 11) in the future depending on the rapidity of warming. *Halicarcinus planatus* is highly abundant around Punta Arenas and Ushuaia, two harbours frequently used for the ships with WAP destination (Cárdenas et al., 2020). Therefore, if the vectors of *H. planatus* persist, ships or rafting, (Aronson et al., 2015; Avila et al., 2020; Hinojosa et al., 2010), some stages (larval, juvenile or adult) may reach the WAP, survive and settle.

SDMs are tuned to generate a simple spatial representation of the occurrence of a species based on environmental variables (Guisan & Zimmermann, 2000; Mateo et al., 2011). Our results rely on a model, that simplifies complex facts (Mateo et al., 2011) and make assumption on future conditions. Beside temperature, ice thickness and salinity, there are many other variables than may vary over time and influence species distribution, such as primary production and ocean currents. Although niche models do not include eco-evolutionary parameters such as adaptation, gene flow or dispersal capacity, they are widely used to provide an insight into present and future species distribution (Thuiller et al., 2004; Titeux et al., 2017). Combining such results with information on biological interactions, physiology, anthropic influence on individual introductions or a complete evaluation of the dispersal capacities of *H. planatus* using a spatial and dynamic approach would fill knowledge gaps about their real invasive capacities in future environmental conditions.

In conclusion, our results suggest that *H. planatus* cannot presently establish in WAP waters, but this situation has a very strong probability to change under projected climate change in the 21st century. While the full consequences of Antarctic warming are yet to be realised, some changes in the distribution and composition of communities have already been observed (Ashton et al., 2017; Clark et al., 2019; Griffiths et al., 2017; Turner et al., 2014). The key for future studies will be to track species distribution and demographic shifts directly as warming continues, to help understand and mitigate marine biological impacts on Antarctic coastal ecosystem.

Acknowledgements

The research was supported by projects FONDECYT Regular 1161358 to KG and EP, INACh DG 14-17 and Chilean national doctoral scholarship CONICYT 21151192 to ZLF, Fondap-IDEAL 15150003 to ZLF and LV, PIA CONICYT ACT172065 to EP and KG, and FONDECYT 1160877 to LV. This study was supported by a "Fonds pour la formation à la Recherche dans l'Industrie et l'Agriculture" (FRIA) and "Bourse fondation de la mer" grants to C. Guillaumot. This study is a contribution to the French Polar Institute and LTSER Zone Atelier Antarctique et Subantarctique (ZATA) program PROTEKER (n°1044).

This is contribution no. 48 to the vERSO project (www.versoproject.be), funded by the Belgian Science Policy Office (BELSPO, contract n°BR/132/A1/vERSO). The research was also financed by the "Refugia and Ecosystem Tolerance in the Southern Ocean" project (RECTO; BR/154/A1/RECTO) funded by the Belgian Science Policy Office (BELSPO), this study being contribution number 25.

We are thankful to Renato Borras, Daniel Ramirez, Yethro Henriquez and Eva Iglesias for help collecting individuals of *Halicarcinus planatus* for the physiological experiment (SCUBA diving work). Thanks to Alejandro Ortiz (IDEAL), Constanza Ceroni, Aurora Prado, Hermes Galo Andrade (IDEAL), Hans Bartsch (IDEAL), Camille Détrée (IDEAL) and Paola Muñoz for helping install and maintain experiments. Thanks to Hermes Galo Andrade, Jorge Navarro (IDEAL), research line Adaptation of Marine Species (IDEAL), Angelica Saldivia (IDEAL) and Luis Villegas (IDEAL) for the technical support for this project. This article contributes to the SCAR Biology Programme AntEco (State of the Antarctic Ecosystem) for travel funding.

Conflict of Interest

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

Zambra López-Farrán, first author of this paper, participated directly in experimental design, sampling, assembly of the experiments, maintenance of experiments, obtaining data, analysis of results and writing the manuscript.

Charlène Guillaumot, co-first author of this manuscript participated in analysis of results, writing, revision and correction of the manuscript.

Karin Gerard participated directly in sampling, assembly of the experiments, writing, revision and correction of the manuscript.

Luis Vargas-Chacoff participated directly in experimental design, assembly of the experiments, analysis of results, revision and correction of the manuscript.

Kurt Paschke participated directly in experimental design, assembly of the experiments, analysis of results, revision and correction of the manuscript.

Valerie Dulière participated in the analysis of the results, revision and correction of the manuscript.

Bruno Danis participated in the analysis of the results, revision and correction of the manuscript.

Thomas Saucède contributed to the occurrence dataset, participated in the analysis of results and manuscript revision and correction.

Elie Poulin participated directly in the project and experimental design, sampling, analysis of the results, revision and correction of the manuscript.

Jonathan Waters participated in the analysis of results, and manuscript revision and correction.

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Figure 1. Male (a) and female (b) specimens of *Halicarcinus planatus* (Fabricius, 1775) collected in the Magellan Strait. Scale: 1 cm. Photo credit to C. Ceroni and K. Gérard.

Figure 2. Presence (red dots) and absence (yellow dots) records of *Halicarcinus planatus* in the Southern Ocean updated by the present study.

Figure 3. Survival rates of adults of *H. planatus* at different temperatures over 90 days.

Figure 4. Survival rates of adults of *H. planatus* at different salinities over 39 days.

Figure 5. Survival rates of larvae of *H. planatus* for 12 days at different temperatures.

Figure 6. Partial dependence plots for the four environmental descriptors that contributed the most to the model. Scaled density distribution of the marginal effect of the descriptors of the model, data points (grey) fitted with a generalized additive model (GAM, blue line).

Figure 7. SDM projections of presence probability (between 0 and 1) for *Halicarcinus planatus* projected under current environmental conditions [2000-2014] for the entire Southern Ocean (A), and with a focus on southern South America, the Scotia Arc and the West Antarctic Peninsula (WAP) (B), the WAP alone (C) and the Kerguelen Plateau (D). Black pixels correspond to extrapolation areas for which projections are not reliable and were removed from projections (according to the Multivariate Environmental Similarity Surface index, MESS).

Figure 8: SDM projections of presence probability (between 0 and 1) for *H. planatus,* projected under environmental conditions IPCC RCP 2.6 climate scenario for 2050 for the entire Southern Ocean (A), with focus on southern South America, the Scotia Arc and the Western Antarctic Peninsula (WAP) (B), the WAP alone (C), and the Kerguelen Plateau (D). Black pixels correspond to extrapolation areas for which projections are not reliable and were removed from the projection (according to the Multivariate Environmental Similarity Surface index, MESS).

Figure 9: SDM projections of presence probability (between 0 and 1) for *H. planatus* projections under environmental conditions IPCC RCP 2.6 climate scenario for 2100 for the entire Southern Ocean (A), with focus on southern South America, the Scotia Arc and the Western Antarctic Peninsula (WAP) (B), the WAP alone (C), and the Kerguelen Plateau (D). Black pixels correspond to extrapolation areas for which projections are not reliable and were removed from the projection (according to the Multivariate Environmental Similarity Surface index, MESS).

Figure 10: SDM projections of presence probability (between 0 and 1) for *H. planatus* projected under environmental conditions IPCC RCP 8.5 climate scenario for 2050 for the entire Southern Ocean (A), with focus on southern South America, the Scotia Arc and the Western Antarctic Peninsula (WAP) (B), the WAP alone (C), and the Kerguelen Plateau (D). Black pixels correspond to extrapolation areas for which projections

are not reliable and were removed from the projection (according to the Multivariate Environmental Similarity Surface index, MESS).

Figure 11: SDM projections of presence probability (between 0 and 1) for *H. planatus* projected under environmental conditions IPCC RCP 8.5 climate scenario for 2100 for the entire Southern Ocean (A), with focus on southern South America, the Scotia Arc and the Western Antarctic Peninsula (WAP) (B), the WAP alone (C), and the Kerguelen Plateau (D). Black pixels correspond to extrapolation areas for which projections are not reliable and were removed from the projection (according to the Multivariate Environmental Similarity Surface index, MESS).

Table 1. Environmental descriptors used for modelling and sources. Spatial resolution set at 5 arc minutes (around 8 km).

Descriptors	Present	Future	Source
Depth	-	-	GEBCO[1]
Roughness	-	-	Modified from Depth layer, raster R package function terrain
Slope	-	-	Modified from Depth layer, raster R package function terrain
Seafloor mean temperature	2000-2014	RCP 2.6 and 8.5 for 2050 and 2100	BioOracle[2]
Seafloor min temperature	2000-2014	RCP 2.6 and 8.5 for 2050 and 2100	BioOracle[2]
Seafloor max temperature	2000-2014	RCP 2.6 and 8.5 for 2050 and 2100	BioOracle[2]
Seafloor mean salinity	2000-2014	RCP 2.6 and 8.5 for 2050 and 2100	BioOracle[2]
Seafloor min salinity	2000-2014	RCP 2.6 and 8.5 for 2050 and 2100	BioOracle[2]
Seafloor max salinity	2000-2014	RCP 2.6 and 8.5 for 2050 and 2100	BioOracle[2]
Seafloor mean primary productivity	2000-2014	Same as present conditions	BioOracle[2]

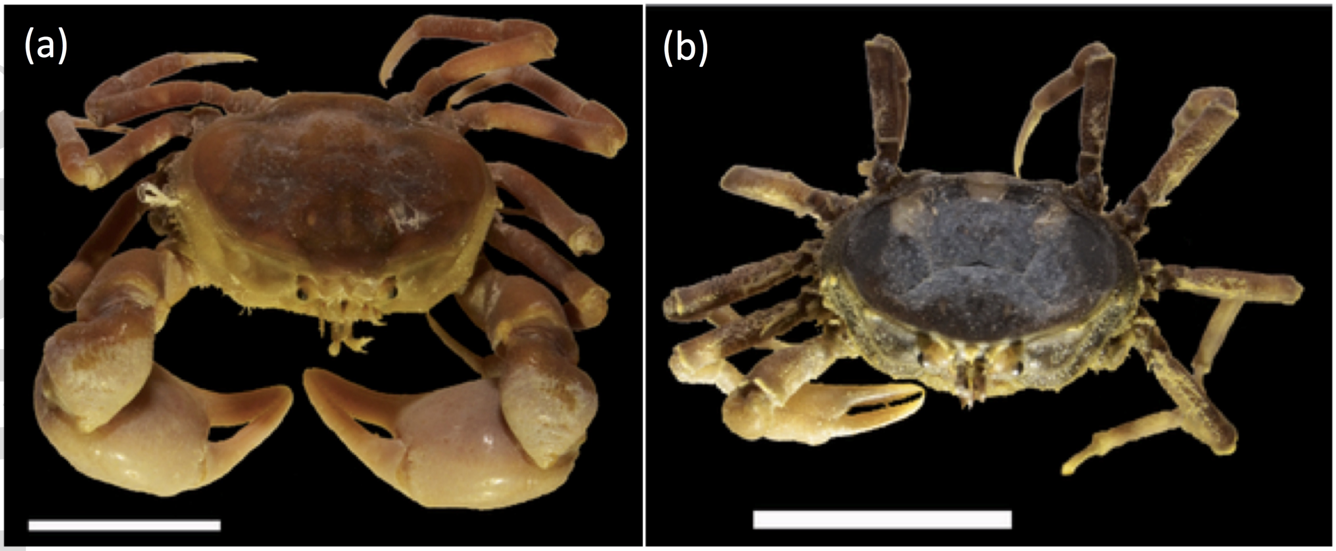
Seafloor min primary productivity	2000-2014	Same as present conditions	BioOracle[2]
Seafloor max primary productivity	2000-2014	Same as present conditions	BioOracle[2]
Ice mean thickness	2000-2014	RCP 2.6 and 8.5 for 2050 and 2100	BioOracle[2]
Ice min thickness	2000-2014	RCP 2.6 and 8.5 for 2050 and 2100	BioOracle[2]
Ice max thickness	2000-2014	RCP 2.6 and 8.5 for 2050 and 2100	BioOracle[2]
Seafloor mean current	2000-2014	Same as present conditions	BioOracle[2]

1. https://download.gebco.net/, accessed February 2020.

2. https://www.bio-oracle.org/index.php, accessed February 2020.

Table 2. Average contribution values and standard deviation (SD) of the 16 environmental descriptors to model projections.

Descriptor	Mean ± SD (%)	Descriptor	Mean ± SD (%)
Mean ice thickness	40.1 ± 3.2	Mean seafloor primary production	0.8 ± 0.1
Mean seafloor temperature	37.8 ± 3.7	Max seafloor primary production	0.5 ± 0.02
Max seafloor temperature	7.6 ± 1.9	Depth	0.5 ± 0.05
Min seafloor temperature	6.9 ± 2.4	Slope	0.2 ± 0.06
Min seafloor salinity	1.4 ± 0.2	Roughness	0.1 ± 0.03
Mean seafloor salinity	1.4 ± 0.1	Max seafloor salinity	0.1 ± 0.03
Mean seafloor current speed	1.3 ± 0.2	Max seafloor primary production	0.001 ± 0.001
Max ice thickness	1.1 ± 0.1	Min ice thickness	0



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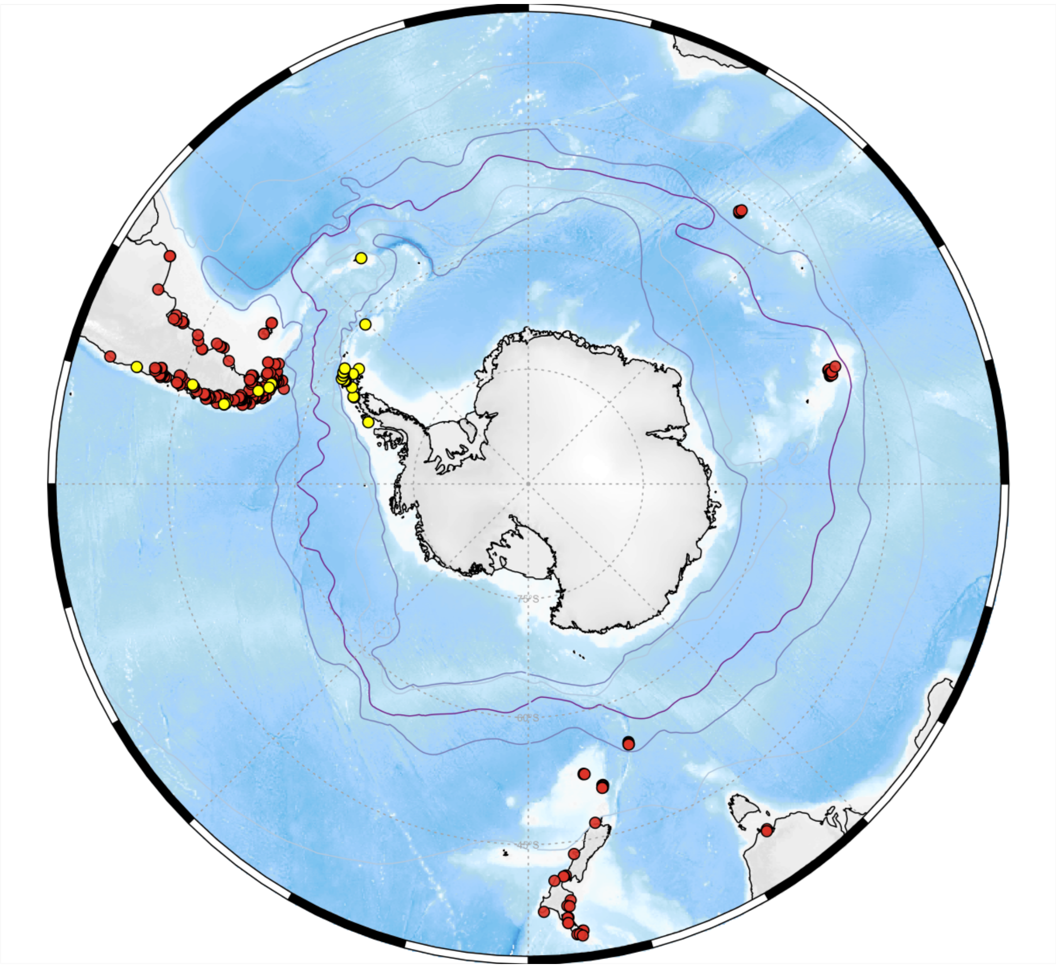

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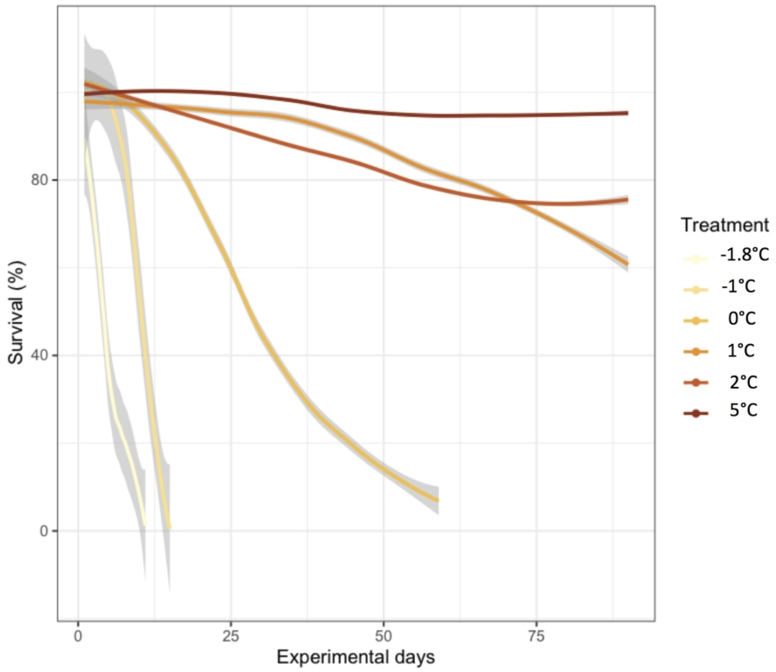

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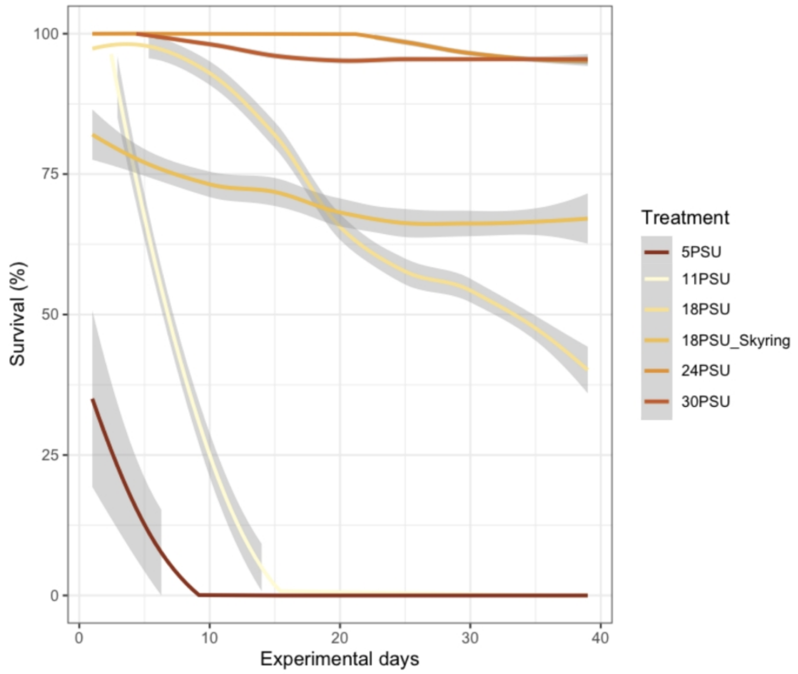

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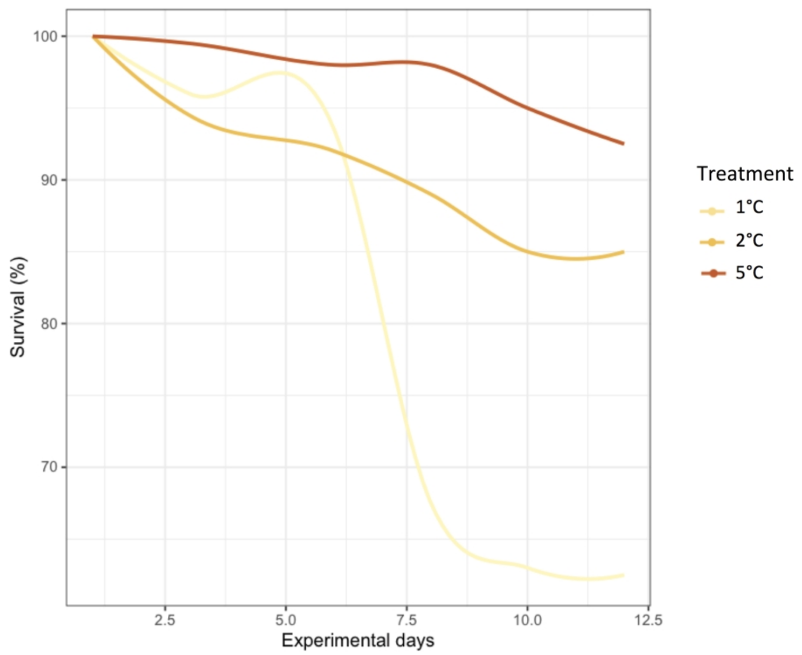

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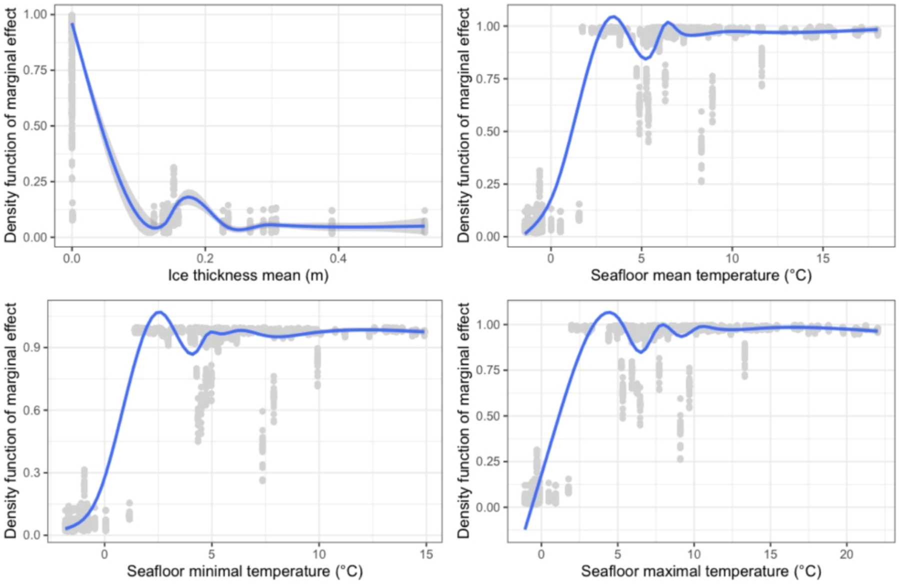

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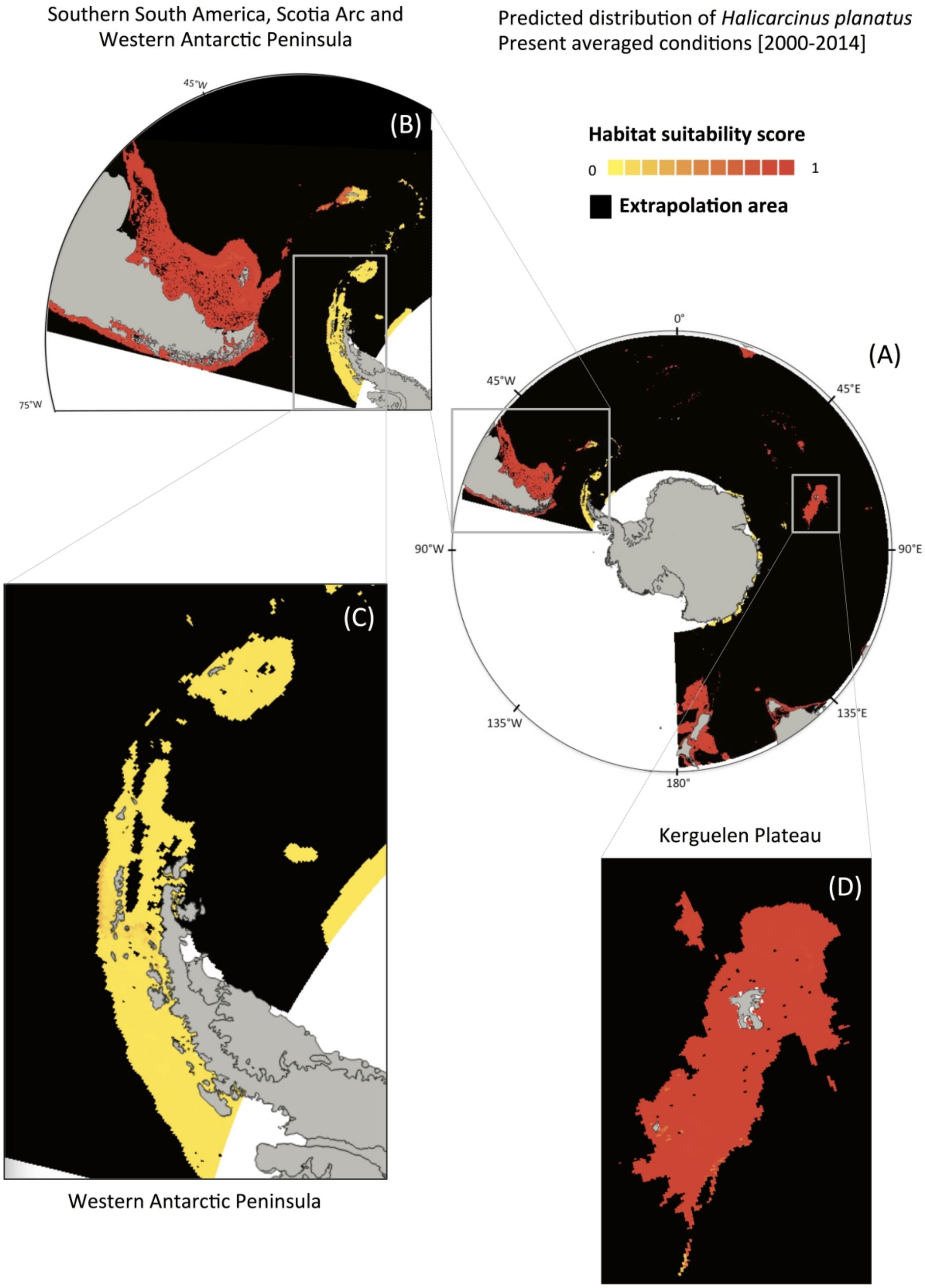

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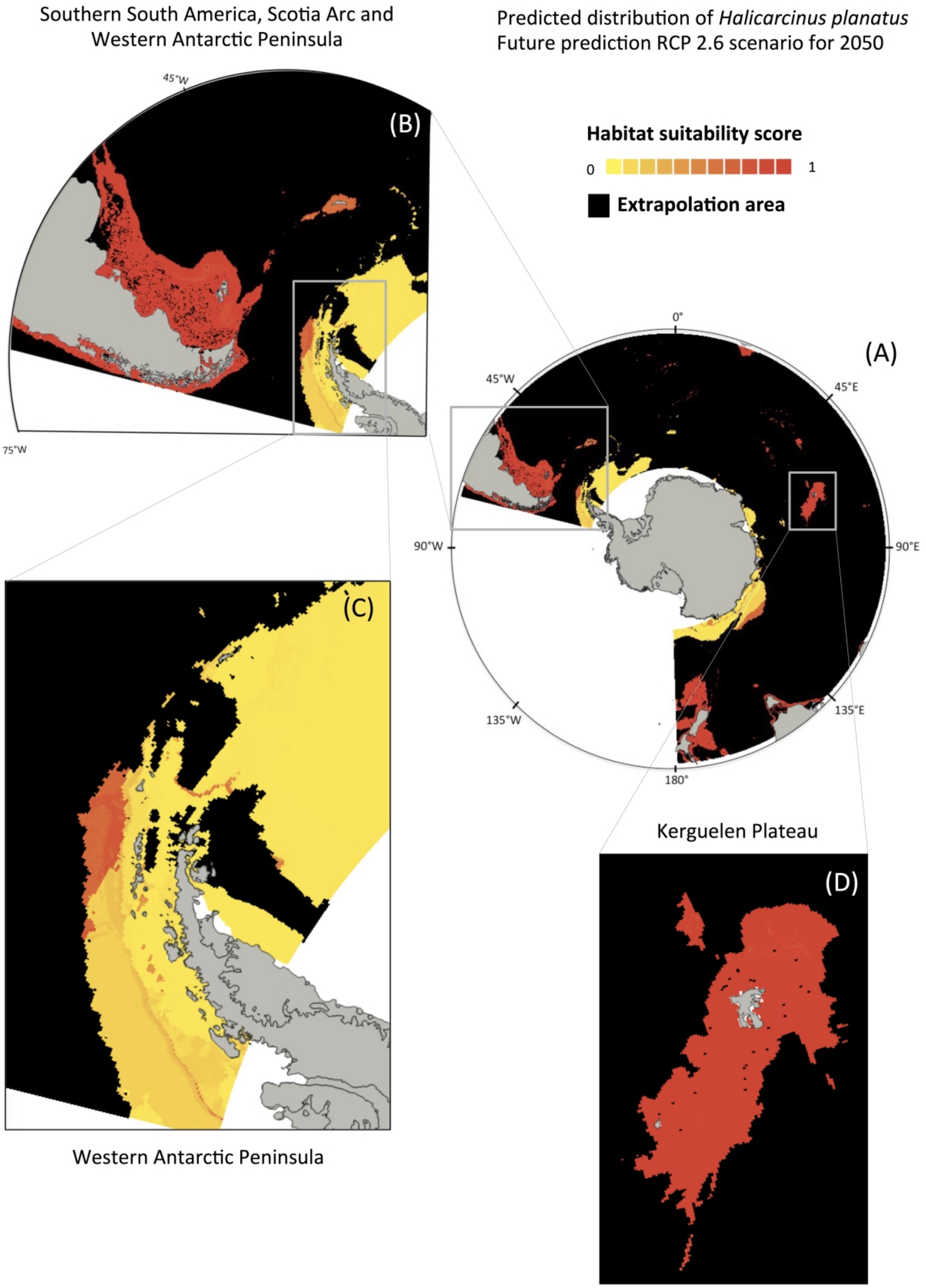

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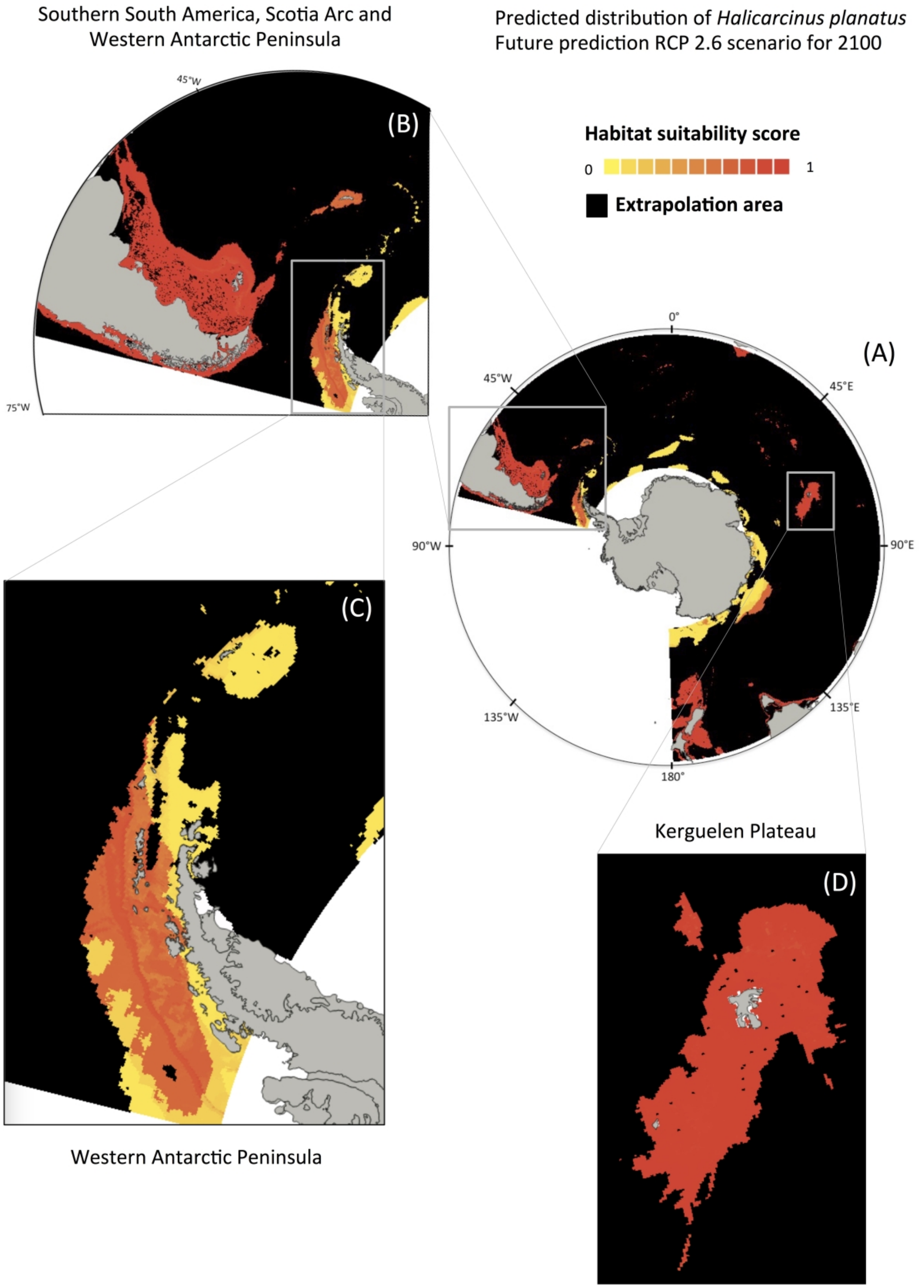

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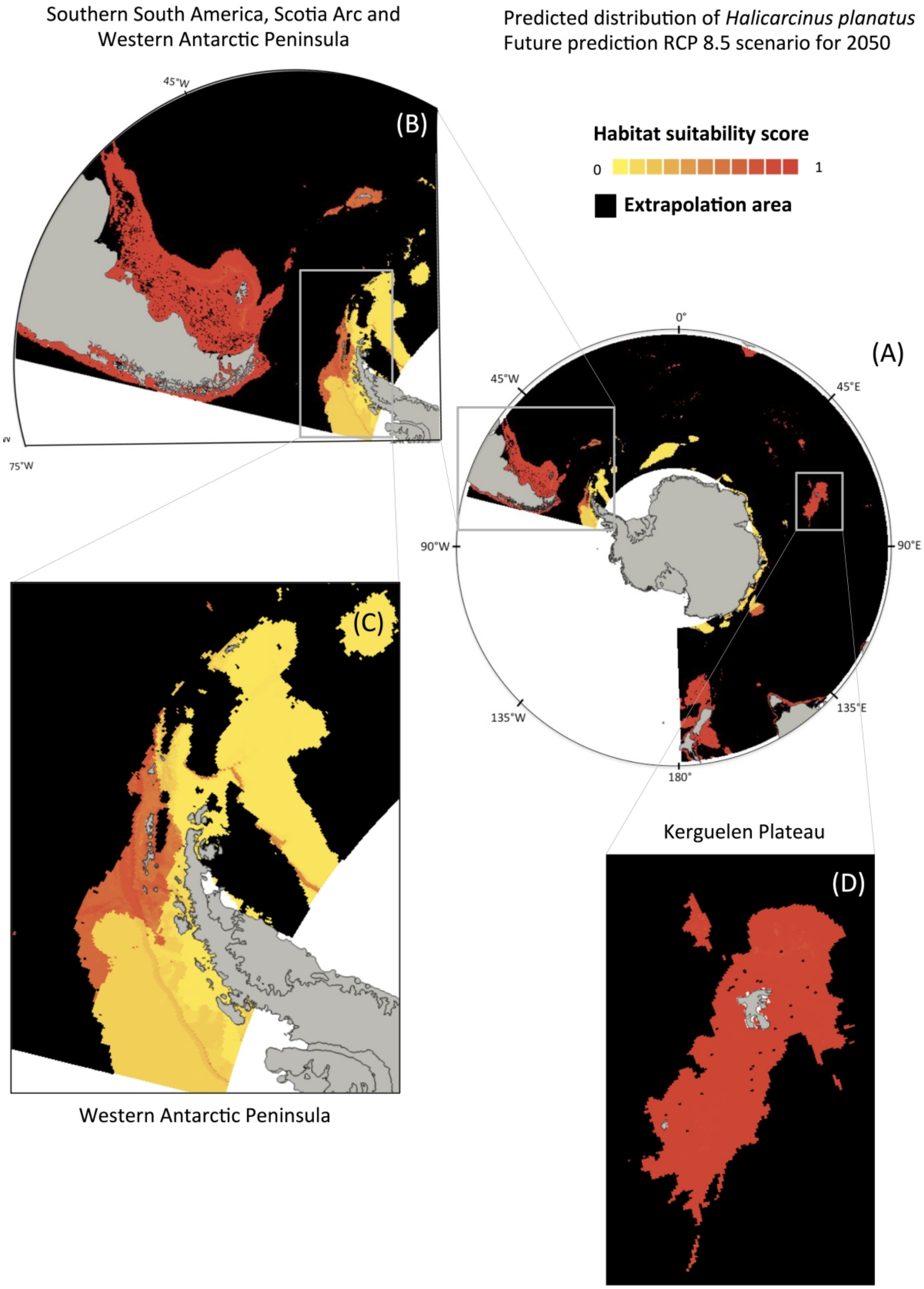

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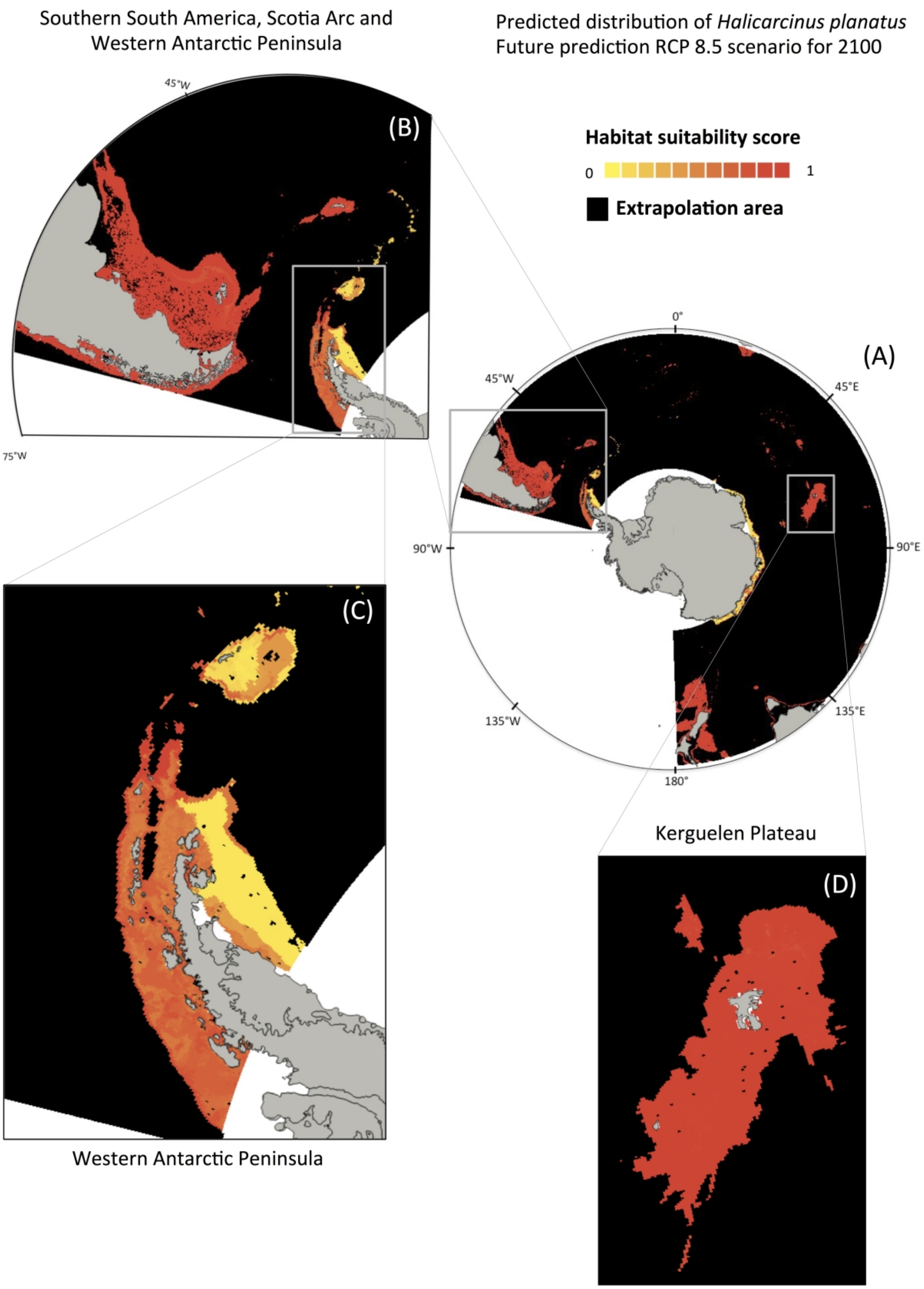

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