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Zambra López-farrán, Charlène Guillaumot, Luis Vargas-chacoff, Kurt Paschke, Valérie Dulière, Bruno Danis, Elie Poulin, Thomas Saucède, Jonathan Waters, Karin Gérard

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**Is the southern crab *Halicarcinus planatus* (Fabricius, 1775)
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Keywords:	Niche modelling, Southern Ocean, Climate Change, Thermotolerance, Survival, Establishment, Reptant Crab, Non-native Species
Abstract:	<p>The potential for biological colonisation of Antarctic shores is an increasingly important topic in the context of anthropogenic warming. Until now, successful Antarctic invasions have been recorded exclusively from terrestrial habitats. While exotic 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 <i>Halicarcinus planatus</i> (Fabricius, 1775), a crab with a circum-Subantarctic distribution and substantial larval dispersal capacity. In 2010, an ovigerous female of this species was found in shallow waters of Deception Island, South Shetland islands. In the present study, a combination of physiological experiments and ecological modelling was used to assess the potential niche of <i>H. planatus</i> and estimate its future southward boundaries under IPCC predictions. We show that <i>H. planatus</i> has a minimum thermal limit of</p>

	<p>1°C, and that its current distribution (assessed by sampling and niche modelling) is physiologically restricted to the Subantarctic region. While this species is thus presently unable to survive in Antarctica, future warming under both best-case and worst-case IPCC scenarios will favour its niche expansion to the Western Antarctic Peninsula by 2100. Future human activity also has potential to increase the probability of anthropogenic translocation of this species into Antarctic ecosystems.</p>

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

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4 Running title: Crab biological expansion into the Antarctic
5

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51

52

53

54 **Abstract**

55 The potential for biological colonisation of Antarctic shores is an increasingly important topic in the context of
56 anthropogenic warming. Successful Antarctic invasions until now have been recorded exclusively from
57 terrestrial habitats. While exotic marine species such as crabs, mussels and tunicates have already been
58 reported from Antarctic coasts, none have as yet established there. Among the potential marine invaders of
59 Antarctic shallow waters is *Halicarcinus planatus* (Fabricius, 1775), a crab with a circum-Subantarctic
60 distribution and substantial larval dispersal capacity. An ovigerous female of this species was found in shallow
61 waters of Deception Island, South Shetland Islands in 2010. A combination of physiological experiments and
62 ecological modelling was used to assess the potential niche of *H. planatus* and estimate its future southward
63 boundaries under IPCC predictions. We show that *H. planatus* has a minimum thermal limit of 1° C, and that
64 its current distribution (assessed by sampling and niche modelling) is physiologically restricted to the
65 Subantarctic region. While this species is thus presently unable to survive in Antarctica, future warming under
66 both best case and worst case IPCC scenarios will favour its niche expansion to the Western Antarctic
67 Peninsula (WAP) by 2100. Future human activity also has potential to increase the probability of
68 anthropogenic translocation of this species into Antarctic ecosystem.

69

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

72

73 **Introduction**

74 Biological invasions are an important component of global change, and one of the most critical global threats
75 to native biodiversity (Sax et al., 2005). According to Richardson et al. (2000), an alien species becomes an
76 invasive species when a set of individuals is able to traverse natural barriers (whether geographical,
77 environmental, or ecological) and subsequently establish in new habitats. While numerous anthropogenic
78 activities can promote invasions, climate change may represent a particularly potent threat to natural
79 ecosystems (Malcolm et al., 2006). Both the rate and dimension of biological invasions are likely to be
80 influenced by global warming (Walther et al., 2009). Understanding the mechanisms and routes of such range
81 shifts may help facilitate the design of strategies for controlling or preventing invasion (Estoup & Guillemaud,
82 2010).

83
84 Notwithstanding the wide expanse of Southern Ocean waters isolating the South American continent from
85 other land masses, several exotic species have been reported in the Antarctic over recent decades (Smith &
86 Richardson, 2011). These examples include the invasive grass *Poa annua* (Chwedorzewska et al., 2015;
87 Molina-Montenegro et al., 2012), seeds of the toad rush *Juncus bufonius* (Cuba-Díaz et al., 2013), the invasive
88 mosquito *Trichocera maculipennis* (Potocka & Krzemińska, 2018), and several South American invertebrates
89 (e.g. insects, worms, freshwater crustaceans; Hughes & Worland, 2010). Alien species have also been
90 reported in marine habitats and in the shallow subtidal zone, in particular in the South Shetland Islands (e.g.
91 decapods and bivalves) and East Antarctica (i.e. bryozoans, hydrozoans, and tunicates) (Avila et al., 2020;
92 Cárdenas et al., 2020; McCarthy et al., 2019). However, there is as yet no evidence for any exotic marine
93 species having established in Antarctica.



94
95 Reaching Antarctic coasts requires dispersal across vast and deep biogeographic barriers that have isolated the
96 continent for millions of years, including traversal of the westward flowing Antarctic Circumpolar Current
97 (ACC) that apparently impedes latitudinal dispersal (Clarke et al., 2005; Rintoul, 2009). The extreme cold
98 temperatures of Antarctic waters (< 5°C) also imply a strong ecophysiological constraint to the survival and

99 development of exotic marine species that have not adapted to near-zero and subzero temperatures (Fraser et
100 al., 2007; Marsh et al., 2001; Peck, 2016) that can reach down to -1.5°C in winter. Consequently, Antarctic
101 marine communities have been considered among the most isolated and endemic on Earth and invasion by
102 exotic species unlikely (Clarke et al., 2005; Griffiths et al., 2009).

103
104 Human activities such as fisheries, tourism and scientific operations rely on direct maritime traffic between
105 Antarctica and lower latitude coasts, including potential transport of alien organisms through ship hull fouling
106 and larval propagules via ballast water (Lewis et al., 2003; Lewis et al., 2005). With more than 50,000 tourists
107 visiting the same west Antarctic spots each southern summer (McCarthy et al., 2019), and 4,000 scientists
108 working in Antarctica during the summer and 1,000 in winter (Hughes & Convey, 2014), tourism and science
109 represent the main vector of Subantarctic propagule pressure on Antarctic communities (Avila et al., 2020;
110 Diez & Lovrich, 2010; Galera et al., 2018; Hellmann et al., 2008; Lee & Chown, 2007; Meredith & King,
111 2005; Tavares & De Melo, 2004). Consequently, records of exotic species in Antarctica are increasing in
112 number, with potential for establishment now primarily constrained by ecological and physiological
113 limitations. As the climate continues to warm, the potential for successful marine invasions into Antarctica is
114 predicted to increase substantially (Galera et al., 2018; Hellmann et al., 2008; Richardson et al., 2000).

115
116 The West Antarctic Peninsula (WAP) is the Antarctic region where the strongest climate warming has been
117 recorded in the continent over the last 50 years (Convey et al., 2009; Gutt et al., 2015; Turner et al., 2014).
118 Seawater and air temperatures have increased by $+1^{\circ}\text{C}$ and $+7^{\circ}\text{C}$, respectively, in the past half-century
119 (Meredith & King, 2005; Schram et al., 2015), with particularly pronounced increases in winter air
120 temperatures (King et al., 2003; Vaughan et al., 2003) and corresponding reductions in sea ice cover (Ducklow
121 et al., 2013; Schofield et al., 2017; Stammerjohn et al., 2012; Turner et al., 2016). Global climate change may
122 cause typically sub-zero Antarctic waters to warm up to (and beyond) zero, potentially providing suitable
123 conditions for the survival of alien species along Antarctic coasts (Galera et al., 2018; Hellmann et al., 2008).

124

125 In February, 2010 an ovigerous female of *Halicarcinus planatus* (Fabricius, 1775) (Brachyura,
126 Hymenosomatidae) was found alive in shallow subtidal waters of Deception Island (WAP; Aronson et al.,
127 2015). *H. planatus* is the only hymenosomatid crab that inhabits shallow waters (Garth, 1958; Varisco et al.,
128 2016) of southern South America and the Subantarctic Falkland/Malvinas, Marion, Crozet, Kerguelen and
129 Macquarie islands (Aronson et al., 2015; Boschi et al., 1969;  fiths et al., 2013; Melrose, 1975; Richer De
130 Forges, 1977). This small crab (carapace width up to 15 mm and 20 mm for female and male, respectively, in
131 Punta Arenas; Fig. 1) is an opportunistic feeder (Boschi et al., 1969), commonly found sheltered under rocks
132 in the intertidal and subtidal zones, in between holdfasts of the giant kelp *Macrocystis pyrifera* or sheltered in
133 hydrozoans and mussel colonies (Chuang & Ng, 1994; Richer De Forges, 1977; Vinuesa & Ferrari, 2008).
134
135 The potential of marine taxa to invade Antarctic waters is likely heavily constrained by ecological and
136 physiological adaptations. *H. planatus* has a strong dispersal potential mediated by an extended planktonic
137 larval stage (Diez & Lovrich, 2010; Ferrari et al., 2011; Richer De Forges, 1977) lasting between 45 and 60
138 days (at temperatures of 11-13 °C and 8 °C, respectively, in the laboratory) prior to benthic settlement (Boschi
139 et al., 1969; Diez & Lovrich, 2010). This species has the physiological capacity to withstand low temperatures.
140 Indeed, while most decapod taxa exposed to cold waters experience increased magnesium ion concentration in
141 the hemolymph ($[Mg^{2+}]_{HL}$), reducing metabolic rate and aerobic activity, potentially leading to death (Aronson
142 et al., 2007; Diez & Lovrich, 2010; Frederich et al., 2001; Thatje et al., 2005), *H. planatus* has the capacity to
143 overcome these issues by reducing $[Mg^{2+}]_{HL}$ (Frederich et al., 2001), providing capacity for survival in cold
144 waters like the Kerguelen Islands, where winter seawater temperatures range between +1.1 and +3.0 °C (Féral
145 et al., 2019). A broad analysis Diez & Lovrich (2010) considering its broad Subantarctic distribution, high
146 dispersal potential and ability to live at low temperatures concluded that *H. planatus* is the most likely future
147 decapod invader  of Antarctic shallow waters.
148
149 Following the recent discovery of a living specimen of *H. planatus* in Deception Island, we evaluate in this
150 study the capacity of the species to settle and invade the WAP and adjacent islands by combining experimental

151 design and a niche modelling approach. Correlative niche modelling approaches have long proved useful to
152 predict the distribution range of species for conservation purposes under stable environmental conditions
153 (Richardson & Whittaker, 2010). However, in the context of climate change, ecophysiological data are
154 required to assess the capacity of organisms to survive under changing environmental conditions. In this study
155 we assessed experimentally the physiological capacity of *H. planatus* to tolerate extreme cold conditions in
156 laboratory, and we evaluated the probability of the species to expand its distribution range southward using a
157 Species Distribution Model (SDM). The modelled distribution of *H. planatus* was first projected under current
158 climatic conditions to evaluate its distribution range in Subantarctic and Antarctic regions. Then the species
159 distribution was modelled under IPCC scenarios RCP 2.6 and RCP 8.5 for 2050 and 2100 to determine the
160 probability that *H. planatus* will colonize Antarctic shallow water habitats in the future.

161

162 **Material and methods**

163 Experimental design

164 Ethical Protocol

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

168

169 Thermotolerance experiments

170 One hundred and twenty adult individuals of *H. planatus* were collected alive in the subtidal zone by SCUBA
171 diving at *Rincón da Bulnes* (RB) (53°35'49.91"S, 70°56'5.19"W, south of Punta Arenas, Chile) on April 9,
172 2018. Individuals were transported to the IDEAL-CENTER laboratory (Punta Arenas) and distributed into 6
173 containers for the experiment. In each container (Appendix 1) 15 females and 5 males were isolated
174 individually in 1 dm³ glass jars of seawater containing a 2 cm-long PVC tube (2.5 cm diameter). A plastic
175 container of seawater was used for water replacement. Each jar and container were aerated and temperature
176 was controlled by a cooler exchanger (Alpha RA12 and RA8, Lauda-Koenigshofen®, Germany). Individuals

177 were acclimated for 15 days with temperature, salinity and photoperiod adjusted to the sampling location (9
178 °C, 30 PSU, 11hrs light/13hrs dark on April 9, 2018). Individuals were fed every 4 days with thawed and
179 chopped mussels and polychaetes. The next day, 30% of seawater was removed from each jar, sucking the
180 bottom to eliminate faeces and food debris. Recipients were then refilled with clean seawater at the exact same
181 temperature and salinity from the plastic seawater container. The latter was then refilled with new seawater,
182 which had time to reach the specific temperature before the next refill. After acclimatization, temperature was
183 reduced by 0.5 °C every day until it reached a threshold value set at 5°C (control; minimal seawater
184 temperature in Punta Arenas), 2 °C, 1 °C, 0 °C, -1 °C or -1.8 °C, depending on the experiment, which was
185 conducted for 90 days following (Vargas-Chacoff et al., 2009). The different temperature threshold values
186 used in the experiment correspond to subtidal temperatures recorded in Fildes Bay (62°12'11.95"S
187 58°56'37.00"W; King George Island, South Shetland Islands, WAP) which ranged between -1.9 °C and 2.1 °C;
188 summer average 1.2 °C (-0.2 °C to 2.1 °C) and winter average -1.6 °C (-1.9 °C to -1.1 °C) in 2017 (data from
189 IDEAL-CENTER, published by Cárdenas et al. (2020)). The 90 days simulate the duration of winter. Survival
190 was checked each morning, and dead specimens were removed and preserved in 96° ethanol.

191

192 Salinity and larval experiments

193 To assess survival at different salinities, adult individuals of *H. planatus* were collected at the same location
194 (RB) on July 5, 2018, transported to the laboratory and separated in containers. Eighteen females and 4 males
195 were isolated in recipients of 10 dm³ filled with seawater. After a 15-day acclimation period at the same
196 temperature, salinity and photoperiod as the sampling location (5 °C, 30 PSU, 8:16 L:D), individuals were
197 submitted to different salinities of 30 PSU (control 1), 23 PSU, 18 PSU, 11 PSU and 5 PSU for 39 days at 5
198 °C. In parallel, some individuals submitted to natural 18-PSU seawater collected in Skyring Sound
199 (52°33'48.07"S, 71°34'15.54"W) were used as a second control. The previously detailed protocol for feeding
200 and cleaning was followed. Survival was checked every morning and dead specimens were removed and
201 preserved in 96° ethanol.

202 During the salinity experiment, at 30 PSU some individuals released larvae which were subsequently collected
203 and placed in 1 dm³ glass jars (200 larvae in each) filled with seawater at 5 °C, 2 °C and 1 °C for 12 days. Crab
204 larvae were fed daily with newly hatched nauplii. Their survival was checked on days 1, 3, 6, 8, 10 and 12 and
205 on the cleaning day which consists in the complete seawater replacement. Dead individuals were removed and
206 preserved in 96° ethanol.

207

208 Species distribution modelling

209 Species Distribution Models (SDM) are used to predict the distribution of organisms based on the statistical
210 analysis of spatial relationships between environmental conditions and species records (Elith et al., 2006;
211 Peterson, 2003; Peterson et al., 2011). SDMs have been widely used in past decades in various applications,
212 including assessing species potential distribution (Guillaumot et al., 2018; Nachtsheim et al., 2017; Reiss et
213 al., 2011) and evaluating potential changes in predicted suitable areas under environmental shifts (Berry et al.,
214 2002; Engler et al., 2009; Meier et al., 2011; Pearson & Dawson, 2003; Thomas et al., 2004).

215

216 Occurrence dataset

217 The study was limited in latitude and longitude to the minimum area where occurrence records have been
218 reported (Longitude: 70.5°E, 75.5°W, Latitude: 36°S, 70.5°S). Presence and absence data were collected
219 during different sampling expeditions carried out between 2015 and 2019 (PROTEKER 1, 4, 5 and 6, INACH
220 ECA 53, 54 and 55), obtained from collaborators and retrieved from IOBIS and GBIF databases and from the
221 scientific literature (Appendix 2). The georeferencing of each occurrence was verified and for this study
222 repeated geographical points were removed; the identification of collected specimens was checked following
223 current taxonomy (Boschi, 1964). Occurrences located north of 34°S in Chile were not considered, since these
224 points were outside the distribution range of the species and could not be corroborated.

225

226 A DarwinCore-compliant dataset was built using presence and absence data of *H. planatus* occurring on
227 Subantarctic islands and South America between 1948 and 2019. Four types of records were included:

228 individualized by specimen, by groups, records obtained from bibliographic reviews and absence records. The
229 dataset is published in GBIF (GBIF, 2018; Lopez et al. 2020).

230
231 Distribution models were built using 314 presence records of both adults and larvae, and 57 absence records
232 (Fig. 2, Appendix 2).

233
234 Environmental datasets

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

243
244 Species distribution was also modelled according to IPCC (Intergovernmental Panel on Climate Change) RCP
245 2.6 (low greenhouse gas concentration levels with a mid-century peak and reduction by 2100) and RCP 8.5
246 (high greenhouse gas concentration levels with increasing emissions over time) scenarios for future decades
247 2040-2050 and 2090-2100 (IPCC, 2013). The RCP 2.6 scenario (Appendix 3) predicts an increase of mean
248 seafloor temperatures of up to +0.7 °C along the Argentinian coast by 2100, +1.3 °C in the Weddell Sea
249 region and +1.3°C on the northern Kerguelen Plateau. Salinity is predicted to be less than RCP 8.5, along with
250 a decrease in ice thickness with maximal depletion values of -30 cm in the south of the WAP by 2100. The
251 RCP 8.5 scenario (Appendix 3) for decade 2040-2050 predicts that seafloor waters will warm up by +1 °C
252 along the southern South American coasts and in the Weddell Sea, and for decade 2090-2100 predicts an
253 increase of seafloor mean temperatures of up to +4 °C along the Argentinian coasts, +0.5 to +1 °C in the

254 WAP, up to +3 °C on the northern Kerguelen Plateau and a predicted decrease of -0.5 to -1 °C in insular
255 regions such as South Georgia and the South Orkney Islands. Salinity is predicted to decrease in the
256 Subantarctic and Antarctic regions by -0.1 unit and sea ice thickness to thin up to 1.2 m in some points,
257 resulting in an expansion of ice-free areas (Fig. S3.1) in the Weddell Sea region.

258

259 Primary production and oceanographic current speed for decades 2040-2050 and 2090-2100 were considered
260 unchanged and similar to present-day conditions as there were no predictions available for these parameters.

261

262 In order to spot and remove extrapolation errors, the Multivariate Similarity Environmental Estimate (MESS;
263 Elith et al., 2010) was computed based on presence records (Guillaumot et al., 2019; Guillaumot et al., 2020).

264 The MESS provides an estimate of the range of environmental conditions under which species occurrences
265 were found and used to calibrate the model. It is then used to select areas where model projections will be
266 calculated, dismissing areas where environmental conditions are not met, and where the model extrapolates.

267

268 Model calibration

269 Species distribution models were generated using the Boosted Regression Trees (BRT) algorithm with the
270 following settings; learning rate 0.005; bag fraction 0.9 and tree complexity 4. These settings minimise the
271 model predictive deviance according to the tests generated following Elith et al. (2008) (Appendix 4). The R
272 package 'gbm' was used to run the model (Elith et al., 2008; Ridgeway, 2006). Models were calibrated using
273 presence and absence data. Modelling performance was assessed using a spatial random cross-validation
274 procedure adapted from Guillaumot et al. (2019) using absence records for model calibration (instead of
275 background records). Also considering the limited number of occurrence records available and their patchy
276 distribution at a broad spatial scale, the occurrence dataset was randomly split into 5 spatial parts, with 80% of
277 the dataset used as a training subset and 20% used as a test subset (Elith et al., 2008). The procedure was
278 repeated 20 times to generate a set of 100 model replicates. The proportion of presence and absence data
279 falling into areas predicted as suitable and unsuitable for the species distribution was evaluated to assess model

280 performance. Model performance was also assessed using the Area Under the Curve (AUC; Fielding & Bell,
281 1997), the True Skill Statistics (TSS; Allouche et al., 2006) and the Biserial Correlation metrics (COR; Elith et
282 al., 2006).

283
284 Model outputs
285 Model predictions were projected on the entire study area (Longitude -76°E, 178°W, Latitude -35°S, -68°S)
286 with a focus on areas where the species is mainly reported presently and where it may be expected in the
287 future, in southern South America, the Scotia Arc and the WAP, the WAP alone and the Kerguelen Plateau.

288 289 **Results**

290 Survival rate in the temperature experiment

291 The first specimen died on the next day after reaching the target temperature in the -1.8 °C temperature
292 experiment. Survival rate at -1.8 °C reached 0% on day 11. Survival reached 0% on day 15 at -1.0 °C. Survival
293 rate at 0 °C 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
294 °C on day 90. (Fig. 3).

295 296 Survival rate of adults and larvae in the salinity experiment

297 Survival rate in the salinity experiment at 5 PSU was 0% on day 2. Survival rate at 11 PSU was 0% on day 14.
298 Survival rate was 50% on day 36 and 36% on day 39 at 18 PSU. Interestingly, survival rate was over 50%
299 (67%) for the experiment at 18 PSU performed with seawater from Skyring Sound. Survival rates were 95%
300 on day 39 at 25 PSU and 30 PSU (Fig. 4).

301
302 Females collected on July 5 were ovigerous and released larvae at the end of August at 5 °C, 30 PSU and 25
303 PSU. The survival rate of larvae at 1 °C was 62.5% on day 12. Survival rates at 2 °C and 5 °C were 85% and
304 92.5%, respectively, on day 12 (Fig. 5).

305

306 SDM predictions under current environmental conditions [2000-2014]

307 SDMs showed very high AUC scores of 0.947 ± 0.059 , TSS of 0.795 ± 0.123 and biserial correlation COR of
308 0.873 ± 0.070 . Correctly classified test data also reached high scores ($89.9 \pm 0.3\%$ for presence test records
309 and $92.9 \pm 2.2\%$ for absence test records correctly classified). The proportion of areas where the model
310 extrapolates is very high (86.3%, Fig. 7) highlighting again the relevance of using the MESS method as
311 recommended by Guillaumot et al. (2019, 2020).

312 Mean sea ice thickness ($40.1 \pm 3.2\%$) and seafloor temperatures are the two main drivers of the species
313 distribution (mean, maximal, and minimal seafloor temperatures with 37.8 ± 3.7 , 7.6 ± 1.9 and $6.9 \pm 2.4\%$
314 contribution to the model, respectively, Table 2), with suitable areas corresponding to low sea ice cover
315 ($<0.1\%$) and minimum temperatures over $+2\text{ }^{\circ}\text{C}$ (Fig. 6). These environmental values match perfectly with the
316 latitudinal partition in the distribution of *H. planatus*, with warmer temperatures ($>+2\text{ }^{\circ}\text{C}$) and lower ice
317 coverage ($<0.1\%$) at the lower latitudes associated with most presence records and few absences, and in
318 contrast, colder temperatures ($<+2\text{ }^{\circ}\text{C}$) and thicker sea ice coverage ($>0.1\%$) associated with the single
319 presence reported in the WAP and most absence records. Interestingly, primary production is not a good
320 predictor of the species' distribution ($<1\%$).

321 As occurrence records are mainly distributed in coastal shallow water areas, depth does not contribute much to
322 the model as no contrast in bathymetry values are present in the dataset. Slope and roughness have probably
323 more contrasting values in deep-sea habitats and consequently do not significantly contribute to the model
324 ($<0.2\%$).

325
326 The extrapolation mask importantly reduces the area projected to shallow habitats (Fig. 7). Distribution
327 probabilities predicted by the model were highest in southern South America, New Zealand and Australia and
328 most Subantarctic islands (Kerguelen, Heard, Marion, Bouvet and South Sandwich Islands; Fig. 7A).
329 Interestingly, the model predicts an intermediate probability of distribution in South Georgia, for which a
330 single absence was reported (Fig. 2), and a high probability on Heard Island, where no occurrence data has
331 been reported yet.

332 The WAP is predicted as unsuitable to the survival of *H. planatus*, as in the case of Deception Island (Fig. 7C).

333

334 SDM predictions under future environmental conditions

335 SDM future predictions under RCP 2.6 in decades 2040-2050 and 2090-2100 predict low and intermediate
336 probability of *H. planatus* to settle in South Georgia, Elephant Island and the WAP, respectively (Fig. 8.I,
337 8.II).

338 The RCP 8.5 scenario showed an increase in probability for *H. planatus* to survive in the WAP (Fig. 8.III,
339 8.IV). Models predict higher presence probabilities in South Georgia and the South Shetland Islands for both
340 decades 2040-2050 and 2090-2100, with the highest values predicted in the northern tip of the South Shetland
341 Islands. The South Orkneys are not predicted as suitable by 2040-2050, but some patches of suitable areas
342 appear by 2090-2100.

343

344 **Discussion**

345

346 This study combines physiological and ecological modelling approaches to highlight the increased risk of
347 marine incursions into Antarctic coastal ecosystem over the coming century. Specifically, we reveal that the
348 widespread Subantarctic decapod *H. planatus* has significant potential to establish in Antarctic waters under
349 realistic climate change scenarios in the coming decades. More broadly, this prospect of future marine
350 invasions of Antarctic ecosystem potentially has crucial implications for the conservation of endemic Antarctic
351 coastal assemblages. Indeed, over recent decades an increasing number of alien marine taxa have been
352 reported from Antarctic ecosystem, including: *Rochinia gracilipes* in the South Shetland Islands (Griffiths et
353 al., 2013); *Bugula neritina* (Bryozoa) off Dronning Maud Land (East Antarctica) in the 1960s (McCarthy et
354 al., 2019); *Hyas araneus* (Decapoda) from Elephant Island in the 1980s (McCarthy et al., 2019); *Ectopleura*
355 *crocea* (Hydrozoa) off Dronning Maud Land and off Queen Mary Land (East Antarctica); and *Ciona*
356 *intestinalis* (Ascidiacea) off Dronning Maud Land (East Antarctica) in the 1990s (McCarthy et al., 2019).
357 Newer records since 2000 include *Emerita* sp. and *Pinnotheres* sp. (larval stage) in King George Islands in the

358 2000s (Thatje & Fuentes, 2003); *H. planatus* from Deception Island (Aronson et al., 2015); *Membranipora*
359 *membranacea* (Bryozoa) and *Macrocystis pyrifera* (Brown algae) from Deception Island (Avila et al., 2020);
360 *Durvillaea antarctica* (Brown Algae) from King George Island (Fraser et al., 2018) and Livingston Island
361 (Avila et al., 2020); and *Mytilus* cf. *platensis* (Bivalvia) in King George Island (Cárdenas et al., 2020) in the
362 2010s.

363
364 There are potentially several different modes of dispersal for species shifting towards Antarctica. Fraser et al.
365 (2018) and Avila et al. (2020) identified dispersal by rafting on buoyant kelps as a possible mechanism for the
366 arrival of exotic species to Antarctica. The former study also included a Lagrangian analysis to show that
367 particles released from South Georgia and the Kerguelen Islands were able to drift across the Polar Front and
368 reach Antarctic coasts following strong storm events. According to this model, storm conditions may enable
369 buoyant kelps to reach the WAP. Such conditions may not be rare, as remains of the kelp *D. antarctica* were
370 observed onshore in the WAP in 2019 and 2020 (López-Farrán personal observation). Direct observations
371 (from southern New Zealand) of *Halicarcinus* adult individuals associated with *D. antarctica* holdfasts, and
372 also in detached, drifting *D. antarctica* at sea (Waters unpublished data) imply rafting as a direct mechanism
373 for adults of this decapod taxon into Antarctic waters. Anthropogenic activities may also be potential dispersal
374 vectors for this decapod (Avila et al., 2020; Cárdenas et al., 2020) (e.g. via ship hulls, ballast waters, outdoor
375 and personal equipment of tourists or oceanographic equipment of scientists).

376
377 No established alien marine species have as yet been observed in Antarctica, suggesting that physiological
378 barriers may be key in preventing such invasions (Richardson et al., 2000). In this study we combined two
379 independent approaches to define the environmental and geographical boundaries of *H. planatus* distribution
380 under present and future environmental conditions. SDM provides an estimate of a species' 'realised niche'
381 (Hutchinson, 1957; Soberón, 2005, 2010). The thermal limit of *H. planatus* corresponds to the coldest
382 conditions of its Subantarctic distribution, located in the Kerguelen Islands, where subtidal temperature ranges
383 between +1.1 and +3.0 °C during the Austral winter (Féral et al., 2019; Lucas, 1980; Richer De Forges, 1977).

384 This species can therefore potentially endure summer conditions in WAP (1 °C and above) in a wide range of
385 salinity (between 18 PSU and 30-33 PSU), but would not survive during the cold winter months. Our
386 experimental results may indicate that Antarctic seawater temperatures may impede larval development even
387 during the summer, suggesting that this species is not able to complete its development in Antarctica under
388 present conditions.

389

390 *Halicarcinus planatus* has previously been highlighted as a potential invader of Antarctica (Diez & Lovrich,
391 2010), because of its potential to live in cold waters, through regulation of $[Mg^{2+}]_{HL}$. However, the present
392 results demonstrated that this physiological characteristic is not sufficient to survive the sub-zero temperatures
393 that typify current Antarctic winters (Fig. 3). The finding that brachyuran crabs cannot currently establish in
394 Antarctica may also help to explain their extinction from shallow Antarctic habitats from the mid-Miocene,
395 ~14 million years ago, when ACC intensification led to cooling and the establishment of a perennial sea-ice
396 cover in the region (Crampton et al., 2016; Hansen et al., 2013; Thatje et al., 2005; Zachos et al., 2008).
397 Numerous marine lineages including brachyurans, lobsters and sharks disappeared from Antarctic waters,
398 along with most teleosteans except for cold-adapted nototheniids and liparids (Aronson & Blake, 2001;
399 Aronson et al., 2007; Clarke et al., 2004). The simultaneous extinction of these diverse taxa was presumably
400 driven by their lack of physiological tolerance to cold conditions (Aronson et al., 2007; Clarke et al., 2004;
401 Frederich et al., 2001). Together, these data may highlight the crucial role of thermal barriers in preserving the
402 integrity of Antarctic coastal ecosystem.

403

404 Under future warming scenarios with increased seawater temperatures and shortened sea-ice seasons,
405 physiological barriers to Antarctic incursions are projected to weaken. For example, near Palmer Station the
406 ice season decreased by 92 days from 1979/80 to 2012/13 (Ducklow et al., 2013; Meredith & King, 2005).
407 According to IPCC RCP scenarios the WAP will continue to warm (Appendix 3), facilitating the
408 establishment of alien species already arriving. *H. planatus* is not able to establish in the WAP under present
409 conditions because it is not a suitable environment (Table 2, Fig. 6, 7), however this may change in the future.

410 In the South Shetland Islands, the worst scenario RCP 8.5 predicts a decrease in ice thickness, the expansion
411 of ice-free areas (Appendix 3) and a 1 to 2 °C increase of seafloor temperature in 2100, leading to suitable
412 conditions for *H. planatus* establishment. SDM predictions indicate the highest suitability for *H. planatus*
413 presence in South Georgia and some places of the WAP (Fig. 8 IV B and C). The most optimistic climate
414 change scenario RCP 2.6 predicts in 2100 a rise of seafloor water temperature of 0.4 °C in the South Shetland
415 Islands, resulting in intermediate SDM predictions in the WAP and South Georgia (Fig. 8.II B and C). Thus
416 according to these future scenarios, it is just a matter of time before the WAP would reach suitable
417 environmental conditions for *H. planatus*.

418
419 Survival is not the only requirement for the establishment of a species in a new area. A successful invasion
420 also implies developing, reproducing and then dispersing to new places (Richardson, 2000 modified), and
421 active behaviour to escape, feed and mate (Frederich et al., 2001). According to SDM predictions and the
422 thermotolerance experiment, a successful invasion would be possible in an environment at +2 °C. Deception
423 Island is the most active volcanic island of the South Shetland Islands, where many subtidal hydrothermal
424 points and geothermal activity offer various temperatures that could favour the establishment of exotic species
425 (Agusto et al., 2004), converting Port Foster into a key location for alien species colonisation (Aronson et al.,
426 2015; Avila et al., 2020). During 3 scuba diving campaigns between 2017 and 2019 we searched for *H.*
427 *planatus* in several places in the WAP, including where it was collected in 2010 - shallow waters off Baily
428 Head outside the caldera of Deception Island (Aronson et al., 2015), (Aronson et al., 2015)- and other sites,
429 active or not, within the caldera of Deception, Penguins, Paulet, Doumer, King George, Roberts islands,
430 Coppermine Peninsula, Chile Bay in Greenwich Island, among other places, and none were found. This
431 absence agrees with our results, but contradicts the presence of the ovigerous female in Deception Island
432 (Aronson et al., 2015), which would need at least two years to reach pubertal molt, the time required in the
433 Kerguelen Islands (Richer De Forges, 1977). This female certainly would not have grown up *in situ*; this place
434 being on the outer coast under full Antarctic conditions (without geothermal activity or hydrothermal influence
435 typical of the interior of Deception Island). Our results suggest its arrival at the mature stage or maybe the

436 ovigerous stage, implying that its development was completed elsewhere. An arrival through rafting is also
437 unlikely. Early stages of *H. planatus* have been observed in floating kelps (*Macrocystis pyrifera*) in the
438 Internal Sea of Chiloé (Hinojosa et al., 2010), and kelp have been reported in Deception Island (Avila et al.,
439 2020). However, the journey from the Subantarctic area to the WAP implies two years across the SO riding
440 kelps, which is highly improbable. This female was more probably brought through the Drake by ship during
441 the southern 2009-2010 summer.

442
443 The establishment of exotic marine species in Antarctica is an issue that is becoming more ~~and more real~~. The
444 composition of the community may change dramatically according to which species establishes. Antarctica is
445 characterized by the absence of durophagous predators (bony and cartilaginous fishes and brachyurans) and
446 short food webs. Therefore, according to Aronson et al. (2007), the arrival of a reptant crab may affect
447 Antarctic ecology and the biodiversity of the shallow Antarctic. With the arrival of the invasive red king crab
448 *Paralithodes cambraticus* in the Barents Sea, reductions of diversity and benthic biomass were observed as a
449 result of the predation pressure (Falk-Petersen et al., 2011), as well as shifts in interspecific competition
450 (Britton et al., 2018; David et al., 2017) and infection of native species by parasites associated with invaders
451 (Bevins, 2019). Although the effects of invasive species are impossible to measure, the return of durophagous
452 predators such as decapods, chondrichthyans and teleosteans in Antarctic shallow waters is widely feared,
453 because they can cause shifts in benthic communities, modifying trophic relationships and homogenizing the
454 Antarctic ecosystem (Aronson et al., 2015, 2007). However, *H. planatus*, with its small size, opportunistic
455 feeding behaviour and soft exoskeleton, is definitely not a top predator (Boschi et al., 1969). It feeds on
456 phytoplankton remains accumulated at the bottom, such as carrion, detritus, mucopolysaccharides from algae
457 and small soft individuals, even of its own species (López-Farrán, personal lab observation). They are prey for
458 fishes (as *Harpagifer bispinis*, *Patagonotothen tessellata* and *Austrolycus depressiceps*; Diez et al., 2011),
459 birds, crabs and sea stars, among others, and look for refuge among rocks and kelp holdfasts to survive
460 (Chuang & Ng, 1994; Richer De Forges, 1977; Vinuesa & Ferrari, 2008). *H. planatus* is part of the
461 Subantarctic ecosystem, playing a fairly important role in food webs (Diez et al., 2011; Richer De Forges,

462 1977) and may not be devastating for the Antarctic ecological community. Under warmer conditions (2 °C),
463 the increase of seawater temperature would affect the WAP ecosystem more intensively than the arrival of a
464 small soft-shelled detritivorous Brachyura such as *H. planatus* (Ashton et al., 2017; Clark et al., 2019;
465 Griffiths et al., 2017; Turner et al., 2014). An example of a bioengineer species that would change the
466 intertidal and shallow subtidal in the WAP is *Mytilus cf. platensis*, an exotic species record in 2019 (Cárdenas
467 et al., 2020). Mussels have the capacity to provide dense three-dimensional matrices (Alvarado & Castilla,
468 1996) that persist for long periods, constituting a micro-habitat which reduces desiccation during low tides,
469 offering a stress-free space for small fish, invertebrate and alga species (Prado & Castilla, 2006). Therefore,
470 those species that have an engineering role in marine ecosystems would change the habitat of the shallow
471 waters of the WAP as we know them today. If this happens, shallow waters of Antarctic ecosystem would
472 begin to be similar to Subantarctic areas. However, even if this crab is not a top predator or a bioengineer that
473 could generate changes in the environment or the food web, *H. planatus* could compete with endemic species
474 in Antarctica for space, food, niche, among others, and thus affect the populations of local species.

475
476 Antarctic water temperature keeps on rising and stirs up the debate on the potential establishment of incoming
477 species through transport on ship hulls, in ballast waters or on floating kelp (Aronson et al., 2015; Avila et al.,
478 2020). Maritime traffic and tourism have increased (Kruczek et al., 2018; Lewis et al., 2005), raising the
479 pressure of propagules in marine Antarctica, and probably this will continue to increase in next years (Kruczek
480 et al., 2018; Lewis et al., 2005). However, the involuntary introduction of non-native species to the Antarctic
481 Region and the movement of species and/or individuals within Antarctica from one zone to any other are
482 among the highest priority issues considered for the Committee for Environmental Protection (CEP) and the
483 Scientific Committee for Antarctic Research (SCAR). Therefore, a strong effort has been invested to improve
484 the ballast water management of ships in Antarctica and to develop a strategy for biofouling (MEPC, 2011).

485
486 Regardless of whether *H. planatus* individuals are able to reach the WAP by themselves or not, the SDM
487 projected under conditions of IPCC RCP 2.6 or 8.5 climate scenarios indicate that individuals could survive

488 and settle, either sooner (Fig. 8.I and 8.II) or later (Fig. 8.III and 8.IV) in the future depending on the warming
489 rapidity. *H. planatus* is highly abundant around Punta Arenas and Ushuaia, two mandatory harbours for the
490 ships with WAP destination (Cárdenas et al., 2020). Therefore, if the vectors of *H. planatus*, ship or rafting,
491 persist (Aronson et al., 2015; Avila et al., 2020; Hinojosa et al., 2010), some stage (larval, juvenile or adult)
492 will reach the WAP, survive and settle.

493
494 Our results rely on models, which are simplifications of complex facts (Mateo et al., 2011). SDMs are tuned to
495 generate a simple spatial representation of the occurrence of a species based on environmental variables
496 (Guisan & Zimmermann, 2000; Mateo et al., 2011). Although niche models do not include eco-evolutionary
497 parameters such as adaptation, gene flow or dispersal capacity, they are widely used to provide an insight into
498 present and future species distribution (Thuiller et al., 2004; Titeux et al., 2017). Combining such results with
499 information on biological interactions, physiology, anthropic influence on individual introductions or a
500 complete evaluation of the dispersal capacities of *H. planatus* using a spatial and dynamic approach would fill
501 knowledge gaps about their real invasive capacities in future environmental conditions.

502
503 In conclusion, our results suggest that *H. planatus* cannot presently establish in WAP waters, but this situation
504 has a very strong probability to change under standard IPCC warming projections. While the full
505 consequences of Antarctic warming are yet to be realised, some changes in the distribution and composition of
506 communities have already been observed (Ashton et al., 2017; Clark et al., 2019; Griffiths et al., 2017; Turner
507 et al., 2014). The key for future studies will be to track species distribution and demographic shifts directly as
508 warming continues, to help understand and mitigate marine biological impacts on Antarctic coastal ecosystem.

509

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528

529 **Conflict of Interest**

530 The authors declare that they have no conflict of interest.

531

532 **AUTHOR CONTRIBUTIONS**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

880 **Figure 8:** SDM predictions of presence probability (between 0 and 1) for *H. planatus*, projected under
881 environmental conditions for the entire Southern Ocean (A), with focus on southern South America, the Scotia
882 Arc and the Western Antarctic Peninsula (WAP) (B), the WAP alone (C), and the Kerguelen Plateau (D).
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884 projection (according to the Multivariate Environmental Similarity Surface index, MESS). IPCC RCP 2.6
885 climate scenario for 2050 (Fig. 8.I), IPCC RCP 2.6 climate scenario for 2100 (Fig. 8.II), IPCC RCP 8.5
886 climate scenario for 2050 (Fig. 8.III) and IPCC RCP 8.5 climate scenario for 2100 (Fig. 8.IV).

887

888 **Table 1.** Environmental descriptors used for modelling and sources. Spatial resolution set at 5 arc minutes
 889 (around 8 km).
 890

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

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

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

893

894 **Table 2.** Average contribution values and standard deviation (SD) of the 16 environmental descriptors to
 895 model predictions.

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

896

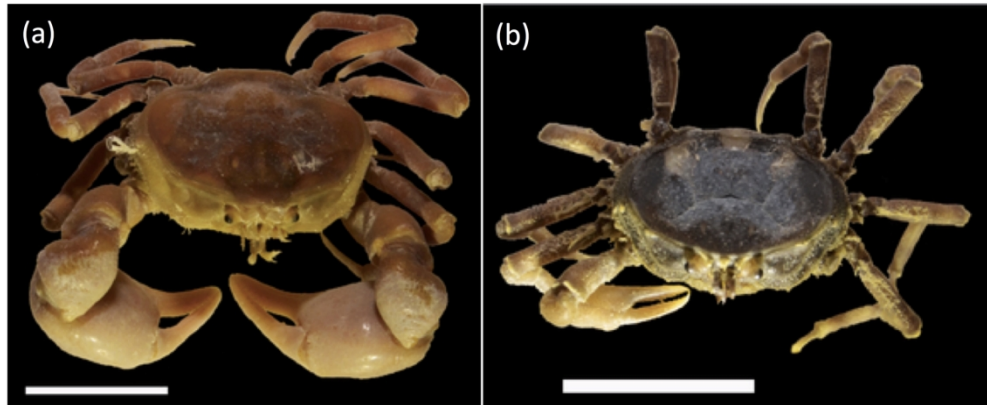


Figure 1. Male (a) and female (b) specimens of *Halicarcinus planatus* (Fabricius, 1775) collected in the Magellan Strait. Scale: 1 cm. Photo credit to C. Ceroni and K.Gérard.

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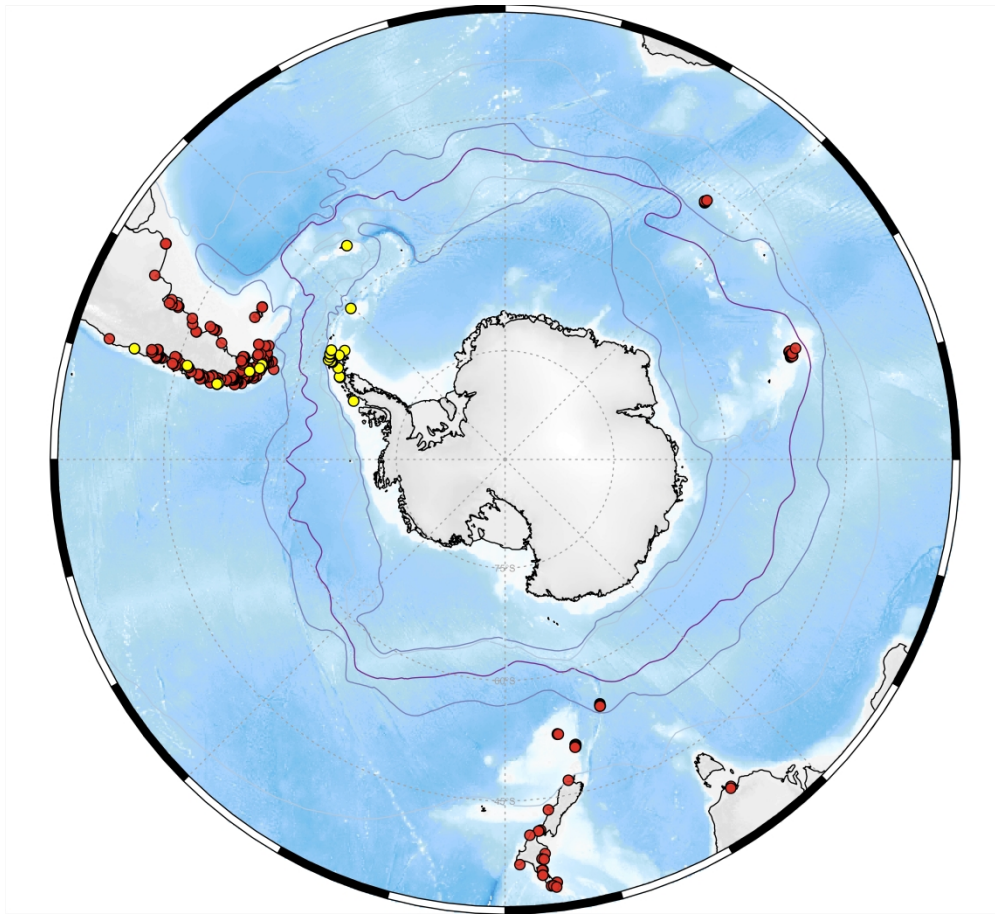


Figure 2. Presence (red dots) and absence (yellow dots) records of *Halicarcinus planatus* in the Southern Ocean used in the present study.

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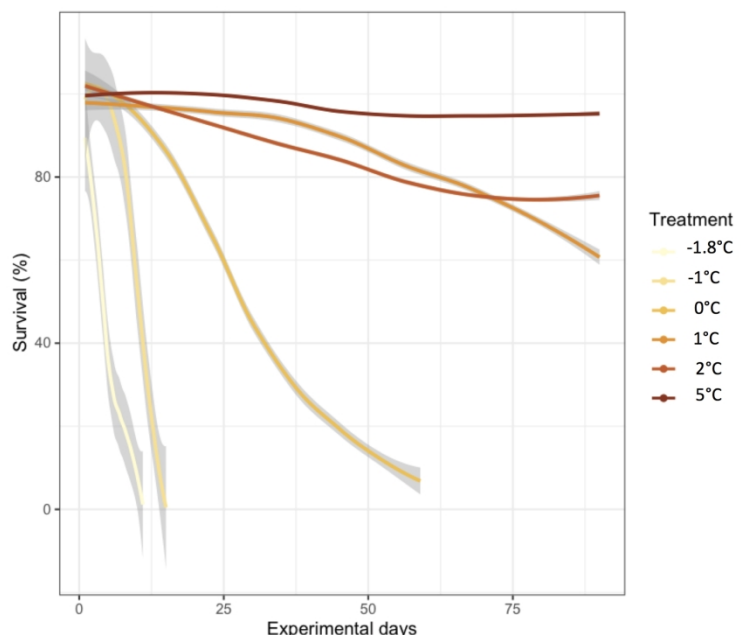


Figure 3. Survival rates of adults of *H. planatus* at different temperatures over 90 days.

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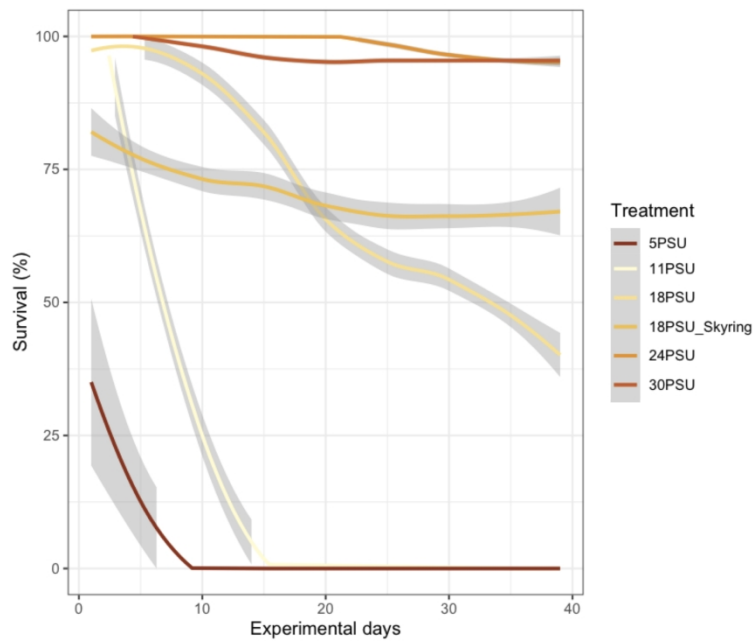


Figure 4. Survival rates of adults of *H. planatus* at different salinities over 39 days.

297x209mm (300 x 300 DPI)

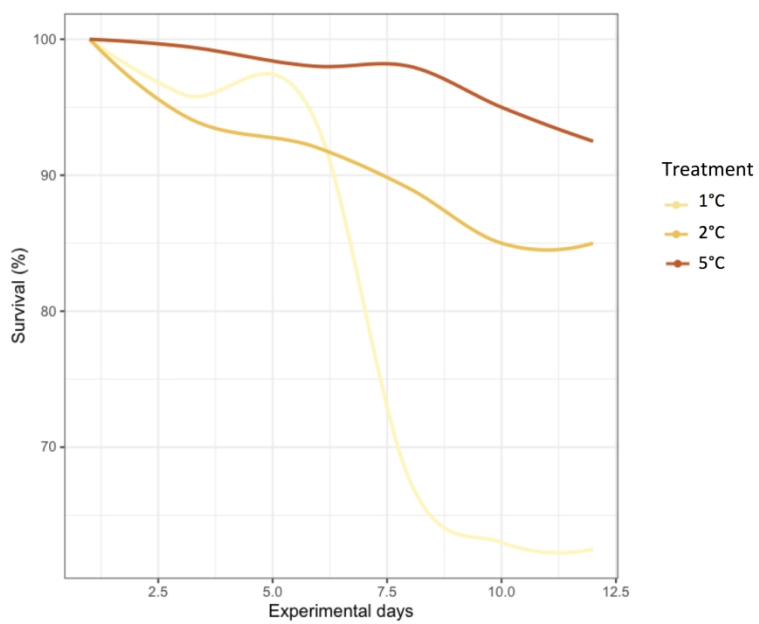


Figure 5. Survival rates of larvae of *H. planatus* for 12 days at different temperatures.

297x209mm (300 x 300 DPI)

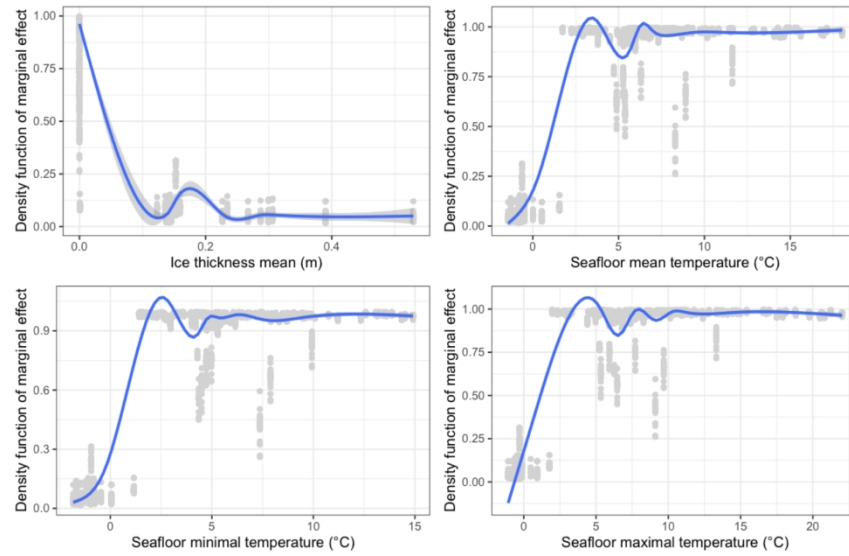


Figure 6. Partial dependence plots for the four environmental descriptors that contribute the most to the model. Scaled density distribution of the marginal effect of the descriptors of the model, data points (grey) fitted with a generalized additive model (GAM, blue line).

297x209mm (300 x 300 DPI)

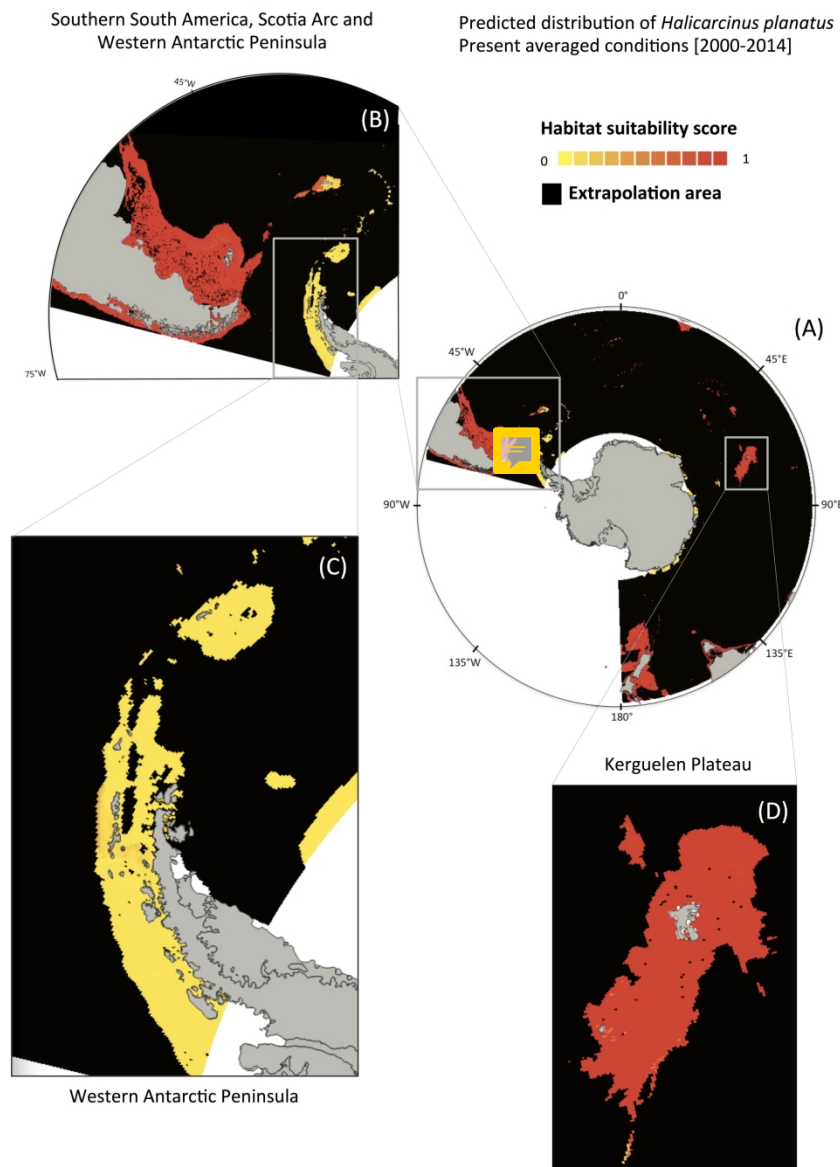


Figure 7. SDM predictions of presence probability (between 0 and 1) for *Halicarcinus planatus*, projected under current environmental conditions [2000-2014] for the entire Southern Ocean (A), and with a focus on southern South America, the Scotia Arc and the West Antarctic Peninsula (WAP) (B), the WAP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

209x297mm (300 x 300 DPI)

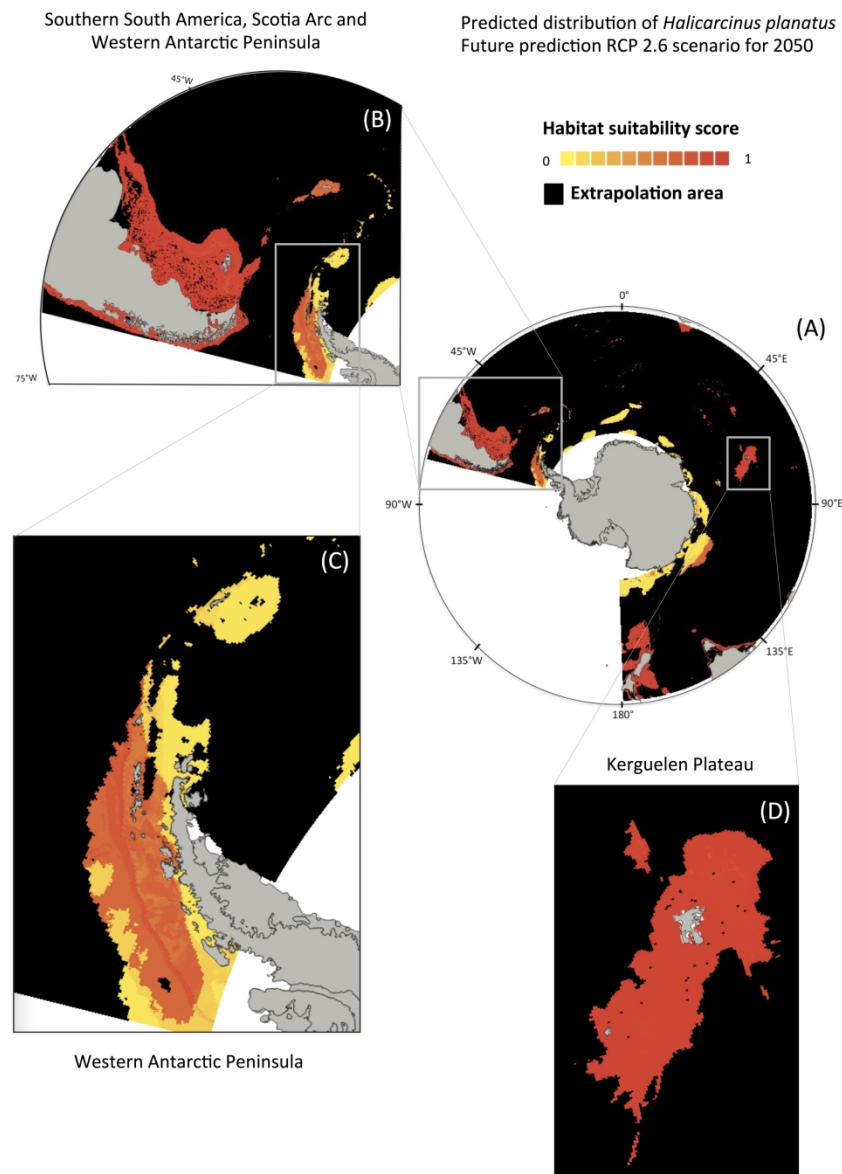


Figure 8: SDM predictions of presence probability (between 0 and 1) for *H. planatus*, projected under environmental conditions for the entire Southern Ocean (A), with focus on southern South America, the Scotia Arc and the Western Antarctic Peninsula (WAP) (B), the WAP alone (C), and the Kerguelen Plateau (D). Black pixels correspond to extrapolation areas for which predictions are not reliable and were removed from projection (according to the Multivariate Environmental Similarity Surface index, MESS). IPCC RCP 2.6 climate scenario for 2050 (Fig. 8.I), IPCC RCP 2.6 climate scenario for 2100 (Fig. 8.II), IPCC RCP 8.5 climate scenario for 2050 (Fig. 8.III) and IPCC RCP 8.5 climate scenario for 2100 (Fig. 8.IV).

209x297mm (300 x 300 DPI)

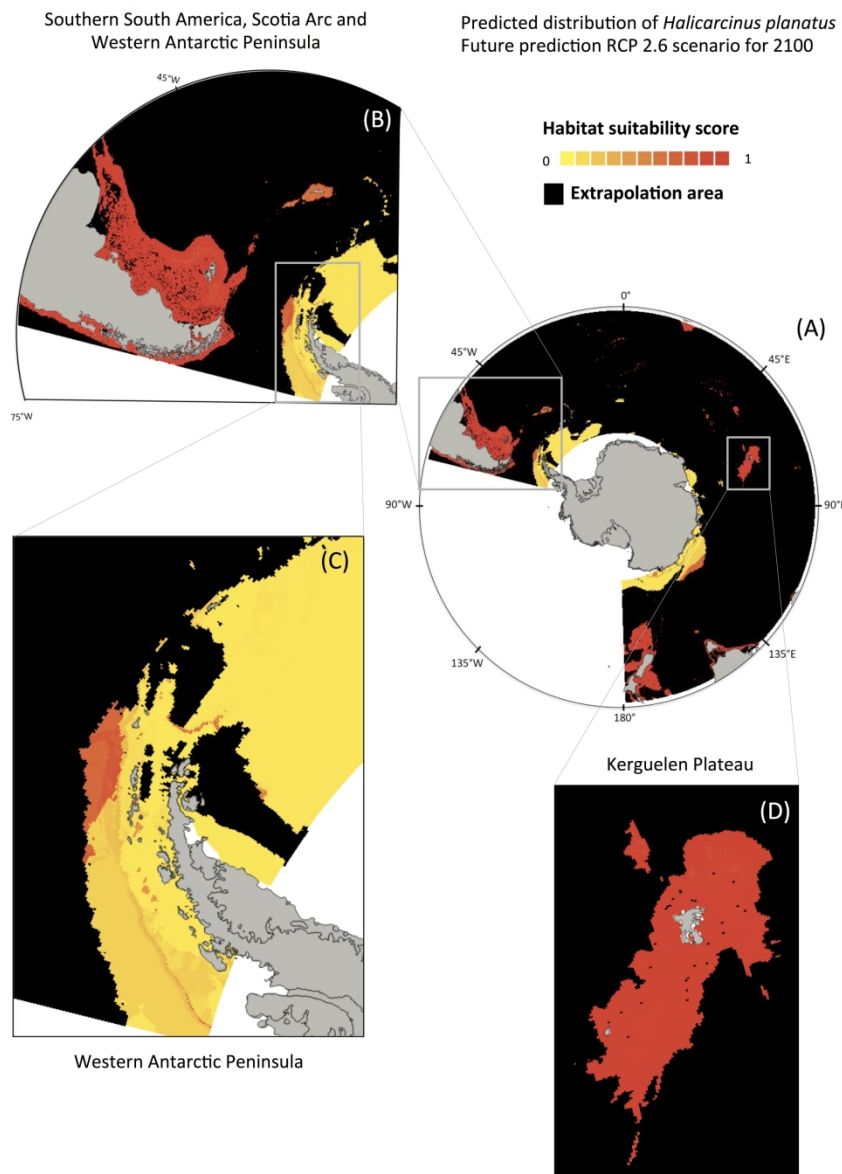


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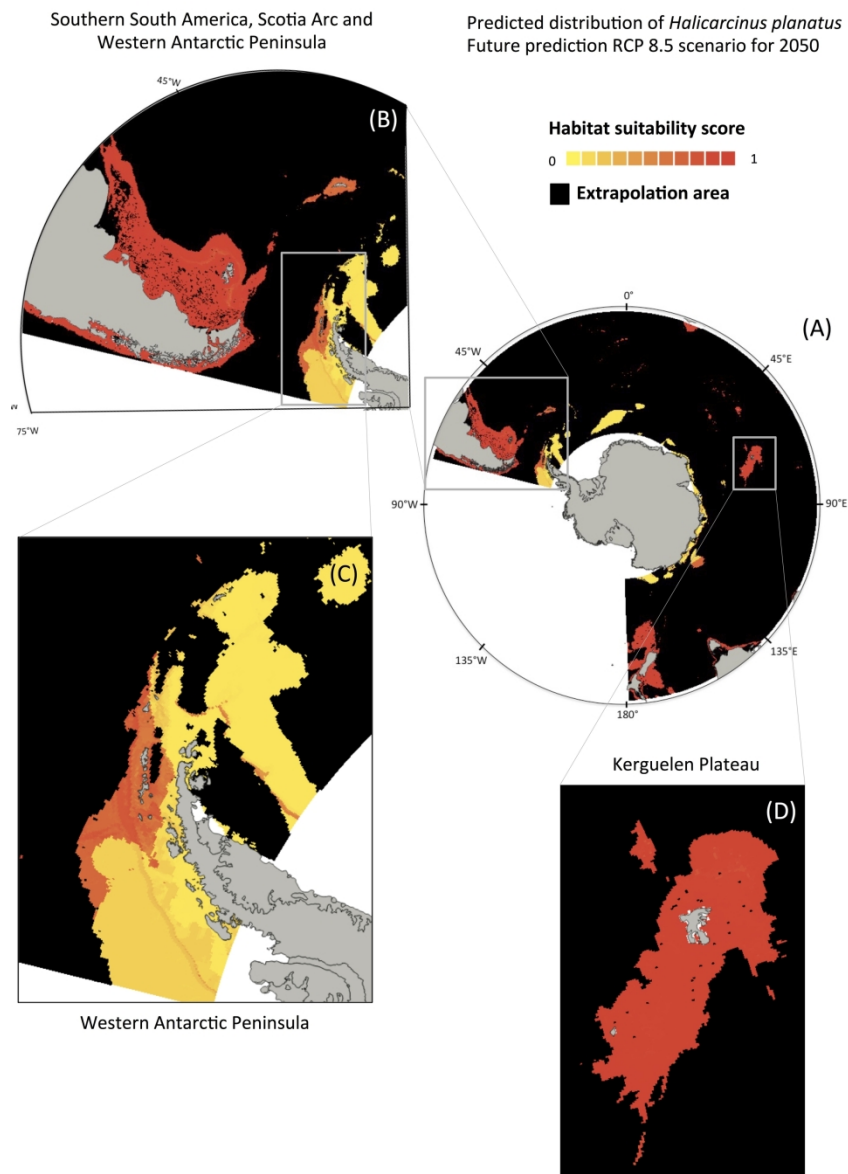


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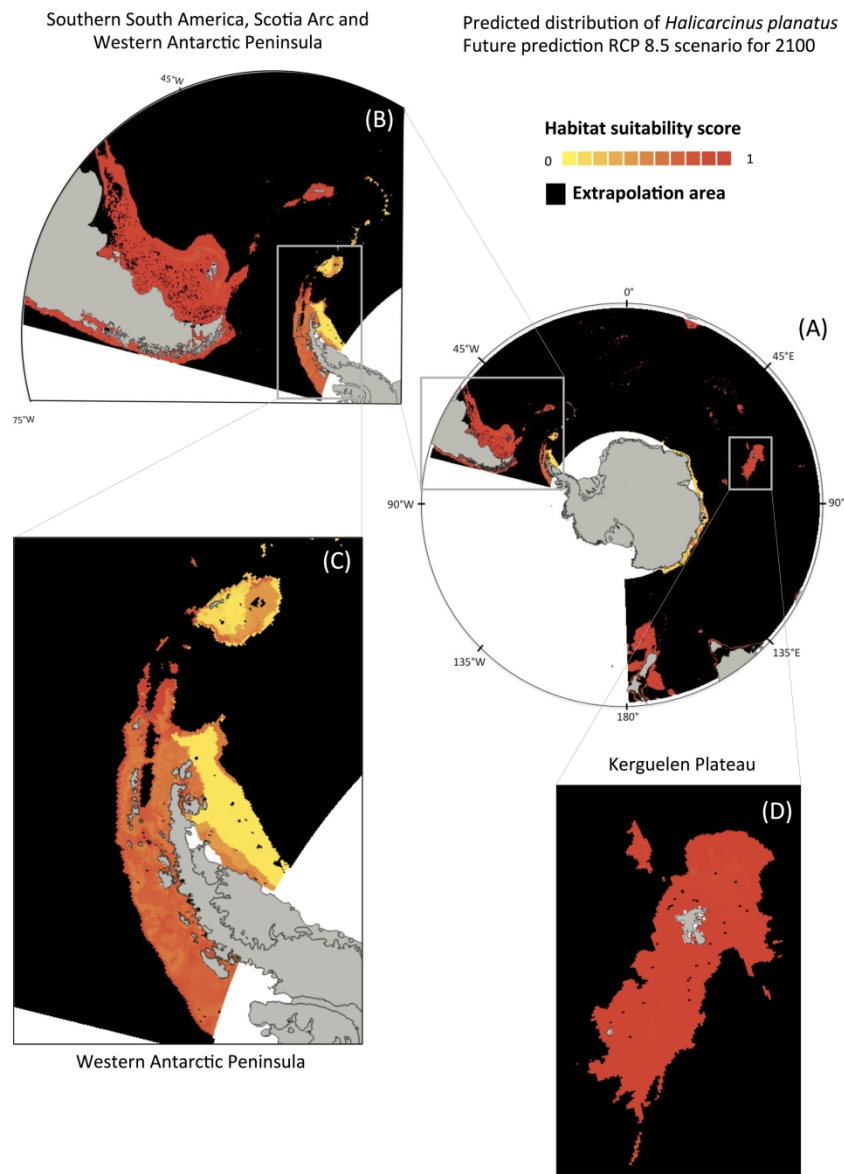


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