

RESEARCH LETTER

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Key Points:

- Sustained increase in ocean temperature and changes in seasonal expansion of sea ice
- Krill habitat is projected to change under different scenarios of chlorophyll *a*
- Localized regions will support future krill spawning and recruitment by the end of this century

Supporting Information:

- Supporting Information S1

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Projected changes of Antarctic krill habitat by the end of the 21st century

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Abstract Climate change is rapidly shaping the living environment of the most abundant keystone species of the Antarctic marine food web, Antarctic krill. Projected future changes for the krill habitat include a sustained increase in ocean temperature and changes in sea ice and chlorophyll *a*. Here we investigate how these factors affect the early life history of krill and identify the regions around Antarctica where the impact will be greatest. Our tool is a temperature-dependent krill growth model forced by data from comprehensive greenhouse warming simulations. We find that by the year 2100 localized regions along the western Weddell Sea, isolated areas of the Indian Antarctic, and the Amundsen/Bellingshausen Sea will support successful spawning habitats for krill. The failure of potentially successful spawning will have a strong impact on the already declining adult populations with consequences for the Antarctic marine food web, having both ecological and commercial ramifications.

1. Introduction

Antarctic krill (*Euphausia superba*) is a key species in the Antarctic marine food web that plays a fundamental role in the transfer of energy between the lower and the upper trophic levels. Over the past five decades it has been a target of increasing demand in commercial fisheries [Ichii, 2000]. Antarctic krill inhabits the Southern Ocean predominantly south of the Polar Front, and its distribution is concentrated in the southwest Atlantic sector, with most of the population residing between 0 and 90°W [e.g., Atkinson *et al.*, 2004, 2008] (Figure 1). Krill early life begins during austral summer, when gravid females lay their eggs in the upper ocean water column [Marr, 1962; Siegel, 2005]. The newly released embryos sink while they develop and hatch to larvae at depths of 700–1000 m (Figure 1a). Subsequently, the larvae ascend and complete development at the ocean surface, where they molt into juveniles before the next summer arrives. Three critical periods of the early life cycle affect their survival most [Ross and Quetin, 1991; Meyer, 2012]: the first period occurs during the development of larvae into the first feeding stage (calyptopis 1, C1) after finishing the descent-ascent cycle [Marr, 1962]. Once at the surface, krill larvae have a narrow window (~10 days) to find food before reaching a starvation threshold (a point of no return) after which the larvae do not survive even if food becomes available [Ross and Quetin, 1989]. The second critical period is during late summer and fall, when food availability allows the larvae to accumulate sufficient lipid reserves. The third critical period comes during the first winter, when they rely on sea ice biota (SIB) as food resource and also use sea ice for shelter [Ross and Quetin, 1991; Daly, 1990; Meyer *et al.*, 2002]. To meet their metabolic demands and grow successfully into juveniles in the following spring, krill larvae need to feed during winter [Meyer, 2012]. Therefore, environmental conditions such as ocean temperature and sea ice extent exert a dominant control over the survival of the larvae. Temperature affects the descent-ascent cycle [Quetin and Ross, 1984] and sea ice influences food and shelter availability during winter [Ross and Quetin, 1991; Daly, 1990; Meyer *et al.*, 2002]; consequently, a retreat of winter sea ice can become a dominant driver of krill population decline [Flores *et al.*, 2012].

Circumpolar Deep Water (CDW), a major water mass in the Southern Ocean generally found below 200 m, is important during krill early life cycle as it affects the development of sinking embryos; any changes in CDW reflect on krill's development [Ross *et al.*, 1988]. Today the temperature at the depth of CDW can reach 2°C south of the Polar front; this particular temperature is favorable for the development of descending krill embryos and the completion of the descent-ascent cycle [Ross *et al.*, 1988]. At such temperatures, the carbon content of krill remaining after the descent-ascent cycle stays above the lower tolerance limit (7.5 μg C), which allows survival of the krill larvae [Ross and Quetin, 1989]. However, as CO₂ emissions continue (RCP8.5), summer sea surface

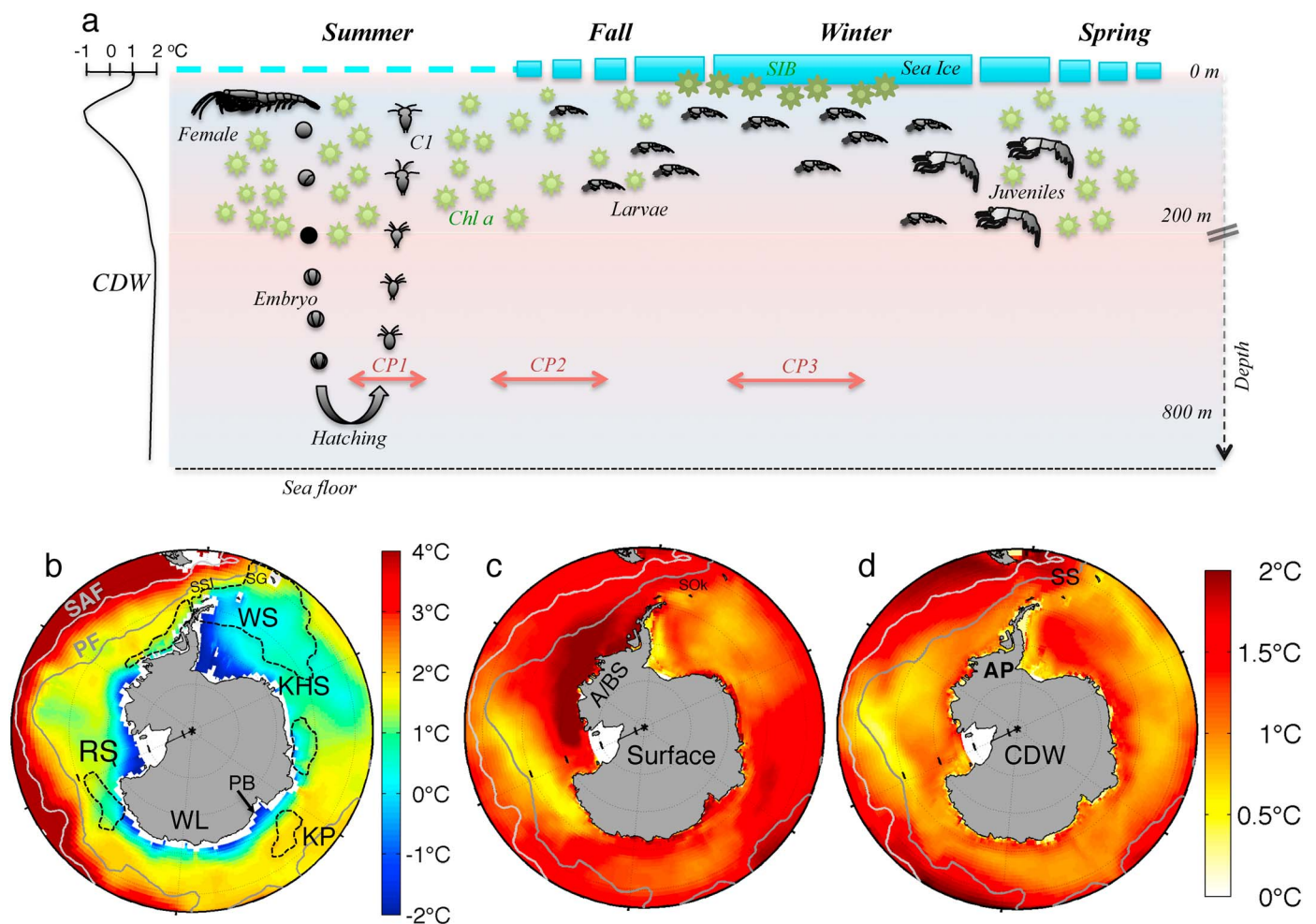


Figure 1. (a) Early life cycle of Antarctic krill. Krill reproduction begins during austral summer; after hatching the embryos develop into nauplii stages to the first feeding stage calyptopis 1 (C1) and after completing the descent-ascent cycle (C1) feed on the available chlorophyll *a* (Chl *a*) during the rest of summer and early fall. The krill overwinter underneath sea ice and molt into juveniles during spring. The three critical periods (CP1, 2, and 3) are indicated; sea ice biota (SIB) available for winter-feeding by krill larvae is also shown. The descent-ascent cycle is influenced by warm Circumpolar Deep Water (CDW), typically found below 200 m. (b) Ocean surface temperature observations from the World Ocean Atlas and regions where the highest abundance of krill is observed (indicated by dashed lines as estimated from Atkinson *et al.* [2004, 2008]). (c, d) Projected changes in temperature (surface and at the CDW depth) for the end of the 21st century. Projections are assessed from a group of 19 climate models under a high-emission scenario (RCP8.5 of CMIP5, section 2). Geographic names and oceanographic features are as follows: CDW = Circumpolar Deep Water, SAF = Subantarctic Front, PF = Polar Front [Sokolov and Rintoul, 2009], RS = Ross Sea, WS = Weddell Sea, KHS = King Haakon VII Sea, A/BS = Amundsen/Bellingshausen Sea, KP = Kerguelen Plateau, SSI = South Shetland Islands, SG = South Georgia, AP = Antarctic Peninsula, SS = Scotia Sea, PB = Prydz Bay, WL = Wilkes Land, SOK = South Orkney.

temperature is projected to increase by 1.5°C on average around the Southern Ocean by the end of the 21st century [Intergovernmental Panel on Climate Change, 2014].

Southern Ocean temperature observations between the 1950s and the 1980s show a sustained increase (0.17°C) at middepth concentrated within the Antarctic Circumpolar Current (ACC) and comparable to Southern Ocean atmospheric temperature changes [Gille, 2002]. Recent assessments of water masses and mixed layer depths [Sallée *et al.*, 2013a, 2013b] from Coupled Model Intercomparison Project Phase 5 (CMIP5) models predict a consistent warmer and lighter water column and a shallow mixed-layer depth. Nevertheless, these warm and light anomalies are stronger in the ventilated layers above the CDW and not at the depths where Gille [2002] observed the sustained increase in temperature.

To investigate the sensitivity of krill early life cycle to projected changes in environmental conditions caused by greenhouse gas emissions and to identify the regions around Antarctica where the impact of those changes on the descent-ascent cycle will be greatest, we utilize a temperature-dependent krill growth model [Hofmann *et al.*, 1992] to estimate hatching depth, development, and carbon utilization during the cycle.

These metrics help evaluate successful spawning habitats and offer insights on the physiological state of krill during the first critical period of survival. To determine the influence of food availability during late summer and fall we also incorporate the observations of surface chlorophyll *a* (Chl *a*) available for krill after completing the descent-ascent cycle, which controls the survival of the larvae during the second critical period. Lastly, to explore the influence of sea ice changes during the third critical period, we estimate the time of sea ice advance in different regions of the Southern Ocean. Our ultimate goal is to make a circumpolar prediction for successful spawning krill habitats that would include the effect of ocean temperature, chlorophyll *a*, and the sea ice date of advance under a high-emission scenario for the end of the 21st century. As part of the prediction we evaluate future changes in the relevant environmental factors in the Southern Ocean using a multimodel ensemble from the CMIP5 data set and incorporate them into our krill growth model.

2. Materials and Methods

2.1. Krill Model

A one-dimensional temperature and density krill growth model was used to simulate the embryo-larvae descent-ascent early life cycle and to estimate development time and carbon utilization [Hofmann *et al.*, 1992; Hofmann and Hüsrevoğlu, 2003]. The model simulates the time-dependent sinking rate of the embryos and ascent rate of larvae (Table S1 in the supporting information). During the descent-ascent cycle the carbon used by the embryo and larva was calculated using a standard conversion constant of 0.385 $\mu\text{g C}$ used per 1 μL of oxygen consumed [Hofmann *et al.*, 1992; Hofmann and Hüsrevoğlu, 2003]. The initial carbon content for the embryo (15 $\mu\text{g C}$) must sustain the embryo during its descent and the larva during the ascent until it reaches the C1 first feeding stage [Ross and Quetin, 1989]. The point of no return for C1 was 7.5 $\mu\text{g C}$ [Ross and Quetin, 1989, 1991]. A detailed description of all relevant parameterizations used for the embryo and larval processes is available in Hofmann *et al.* [1992] and Hofmann and Hüsrevoğlu [2003].

We estimated the successful spawning habitat for krill, taking into account the three critical periods of larval survival [Siegel, 2005] (Figure 1a). For the first period we considered survival of the larvae if the carbon content was higher than 7.5 $\mu\text{g C}$ when reaching the surface; we also require that the bottom depth be greater than the hatching depth, to allow enough depth for the cycle to be completed. In areas of shallow bathymetry the embryos hit the bottom before hatching, which increases the chances for the embryo to undergo predation by benthic organisms or suffer damage [Hofmann *et al.*, 1992; Hofmann and Hüsrevoğlu, 2003]. For the second period we considered larval survival when the C1 larvae encountered chlorophyll *a* concentrations higher than 0.5 mg m^{-3} [Ross and Quetin, 1989, 1991]. To estimate survival during the third critical period, we considered sea ice time of formation (hereafter, date of formation) following a relationship between the timing of sea ice advance and the recruitment success index expressed in values from 0 to 1, where 1 is a 100% recruitment [Quetin *et al.*, 2007]:

$$\text{krill_recruitment_index} = e^{-0.56 \times \text{month_advance}} \quad (1)$$

The highest recruitment index (>0.85) is reached when sea ice forms in March; it is moderate-high (>0.4) when sea ice forms no later than mid April—we considered this latter value as the threshold when estimating successful spawning areas. We used this relationship to account for larval survival after winter, in order to construct the present-day and end of the 21st century circumpolar projections of successful spawning habitats. Projected reductions in percentage of spawning habitats were estimated based on the reduction in the number of grid cells at the end of this century with respect to the beginning of this century.

2.2. CMIP5 Data Sets

Our study aims to consider extreme changes in krill spawning habitats; therefore, to estimate projected changes in the habitats by the end of the 21st century we use projections of temperature and salinity (used to calculate density) from 19 climate models (Table S2) participating in the Coupled Model Intercomparison Project Phase 5 (CMIP5). We use a scenario with high emissions, the Representative Concentration Pathway 8.5 (RCP 8.5), which considers no mitigation over time [Riahi *et al.*, 2011]. This climate scenario is characterized by increasing gas emissions over time leading to high greenhouse gas concentration levels (roughly doubling CO_2 concentration from the present-day level [van Vuuren *et al.*, 2011]). Temperature and salinity projections used in our analyses corresponded to the most commonly used in Southern Ocean studies [Sallée

et al., 2013a, 2013b; Turner *et al.*, 2013; Wang, 2013]. For further details of the krill model and its validation, please refer to the supporting information.

2.3. Observations

The temperature and salinity data sets correspond to monthly climatologies obtained from the World Ocean Atlas 2009 [Locarnini *et al.*, 2010; Antonov *et al.*, 2010] at standard depths (0–4500 m) and horizontal resolution of 1° (latitude-longitude). Averages for austral summer (December to January) were used to force the descent-ascent model. NASA SeaWiFS monthly mean chlorophyll *a* [O'Reilly *et al.*, 2000] for 1997–2002 was used to calculate climatology of chlorophyll *a* concentrations for the end of austral summer and beginning of fall months (January to March); spatial resolution of this data set is 0.5° latitude-longitude. Sea ice date of formation was calculated (see below) using daily sea ice concentration obtained from NOAA/NSIDC climate data record of passive microwave sea ice concentration [Gloersen *et al.*, 1992; Meier *et al.*, 2013] for 2006–2010. An average of sea ice date of formation obtained from observations was used to compute the recruitment index (see section 2.1)

2.4. Sea Ice Estimates

We estimated the sea ice date of formation by defining the sea ice edge as the boundary given by a 15% sea ice concentration threshold [Stammerjohn *et al.*, 2008]. The sea ice day of advance is determined by first defining a search window that begins and ends during mean summer sea ice extent; minimum in mid-February (begins day 46 of year 1 and ends day 45 of the following year or 46 leap year). Within this window the day of advance is identified when sea ice concentration first exceeds 15% for at least 5 days [Stammerjohn *et al.*, 2008]. The day of sea ice retreat is defined when sea ice concentration falls below 15% before the end of the search year [Stammerjohn *et al.*, 2008]. Using this approach, we assessed the time of formation of sea ice, we also estimated the winter sea ice cover at the beginning and end of the 21st century within each climate model (Table S2) and used the results to identify areas of the Southern Ocean where winter sea ice distribution changed. Then, a multimodel ensemble mean of sea ice distribution was constructed.

To account for the large uncertainty in sea ice distribution in the models, we evaluated the number of models for which the sign agrees with the sign of the ensemble mean (Figure S3). The maximum number of models that agree with the mean are 14 out of 18; therefore, we consider the regions wherein 12 or more models agreed as the most robust results in our interpretations. Krill habitat and percentages of increase and decline in krill habitat for both regions (all projected habitat and regions where 12 or more models agree) are shown. Additionally, we consider the 1979–2004 trend map for the day of sea ice advance obtained from satellite measurements of sea ice concentration from the study of Stammerjohn *et al.* [2008] (i.e., their Figure 4a), where they observed a regional change in the day of sea ice advance of approximately a delay of 1 d/yr in the formation of sea ice along the west Antarctic Peninsula (wAP), Amundsen Sea, western Weddell Sea, and along east Antarctica offshore Prydz Bay. Linear extrapolation of this change (~1 d/yr) to 2100 suggests a 90 day delay in the formation of winter sea ice; we also consider earlier retreat by this same trend, as well as an earlier advance and later retreat around the Southern Ocean that are outside the regions previously mentioned. A map of the day of sea ice advance was constructed using these trends and used as an additional approach to assess survival of krill during the third critical period (i.e., section 2.1).

3. Results

Ocean surface and CDW temperatures obtained from using the RCP8.5 scenario are projected to increase 1–1.5°C (Figures 1c and d). The Amundsen and Bellingshausen Seas are the regions with the highest projected surface temperature rise of about 2°C south of the Polar Front (Figure 1c). At the CDW depth, the maximum temperature increase of 0.8–1.3°C is predicted for the Ross Sea, King Haakon VII Sea, and the region north of the South Shetland Island across the Scotia Sea (Figure 1d).

Using the krill model under present-day conditions, we have estimated the regional patterns of successful spawning habitat for krill (Figure 2e). The identified patterns are generally consistent with the observed historical distribution of the habitat occupied by krill adults [Atkinson *et al.*, 2004, 2008]. Within these habitats, the first feeding stage larvae, spawned during summer, completes development when there is still enough chlorophyll *a* at the surface [Meyer *et al.*, 2002; Meyer, 2012], with concentrations typically higher than

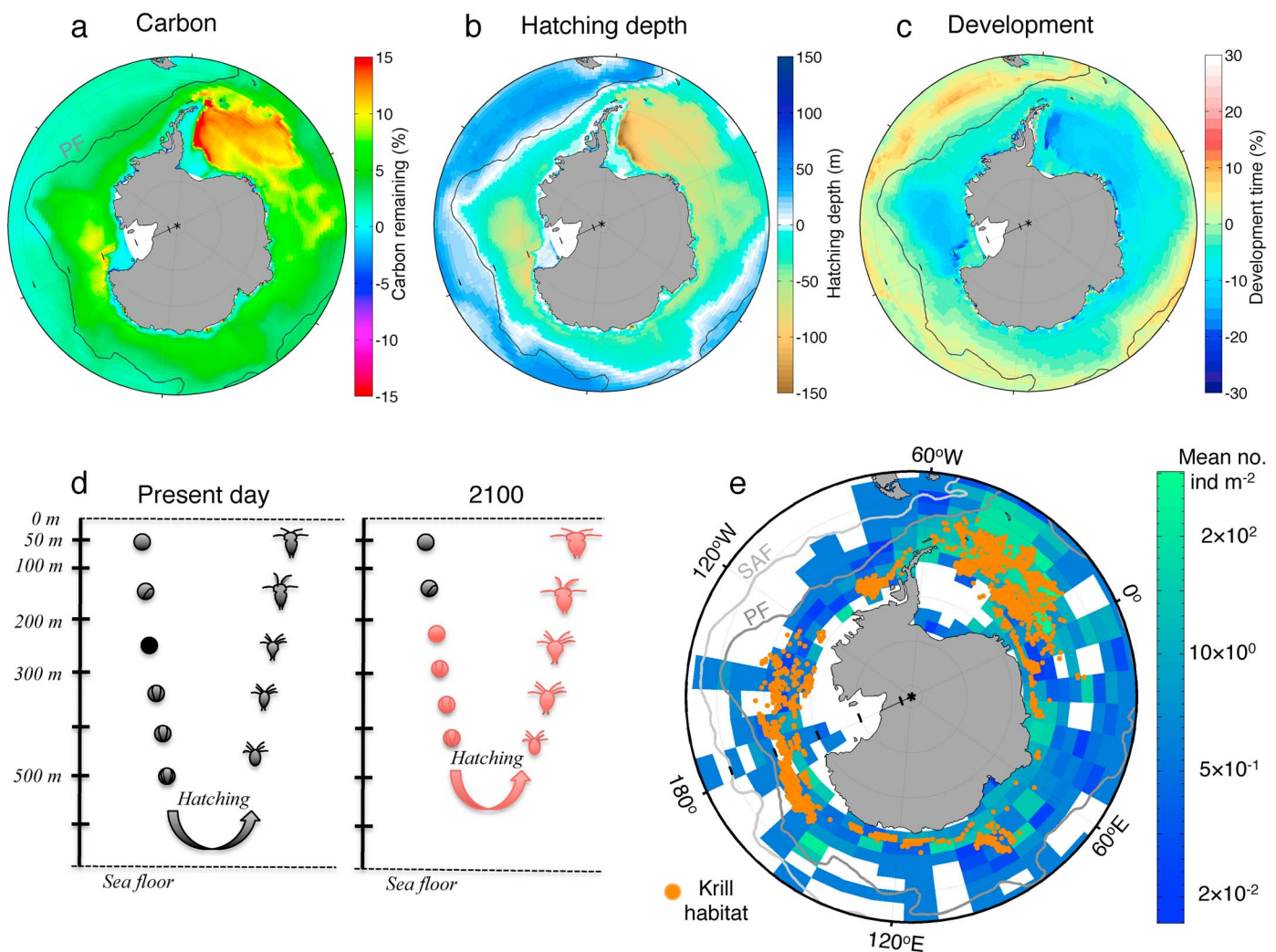


Figure 2. Projected changes (future minus present) in (a) embryo carbon remaining after the descent-ascent cycle, (b) hatching depth, and (c) time to complete development. Positive values of the carbon store change indicate a more favorable condition of the larvae when reaching the surface. Note a general decrease in hatching depth and embryo development time by 2100. (d) Representation of the descent-ascent cycle at present-day conditions of temperature and density and under projected environmental changes expected for 2100. The descent-ascent profile in red shows an accelerated development of the embryo and larvae when reaching warmer than present-day CDW. (e) Recruitment habitat of Antarctic krill at present day as estimated from the modeled descent-ascent early life cycle (orange dots). The model incorporates the effect of temperature and density of the water column, summer chlorophyll *a* availability, and sea ice date of formation. The blue-green-colored map gives the circumpolar distribution of krill adults obtained from historical observations of krill densities stored in the KRILLBASE data archive [e.g., Atkinson *et al.*, 2004, 2008]. The light gray contour shows the mean position of the Subantarctic Front (SAF) and the dark gray contour shows the mean position of the Polar Front (PF).

0.5 mg Chl *a* m⁻³. Further, if sea ice formation occurs no later than mid-April the region is considered a suitable habitat for krill larval survival [Quetin *et al.*, 2007].

The model indicates that carbon utilization during the descent-ascent cycle will decrease by 15% along the western Weddell Sea and about 10% in most of the Ross Sea. In these two regions hatching depth will shoal by 100–150 m and the krill development time will shorten by 10–15% (Figures 2a–2c). Ocean temperature at the depth of CDW will increase (e.g., Figure 1d), accelerating krill development and allowing a successful completion of the descent-ascent cycle in deeper regions of the Southern Ocean, so that ascending larvae are able to reach the ocean surface right before the first feeding stage (Figure 2d).

The timing of sea ice advance is crucial for the growth of sea ice microbial communities that provide larval krill with an alternative food source when food in the water column is scarce during winter [Quetin and Ross, 2001]. When sea ice forms earlier, high abundances of phytoplankton from the fall bloom are easily incorporated into the ice lattice and, in addition, more sunlight is available for the ice algae to grow before winter comes.

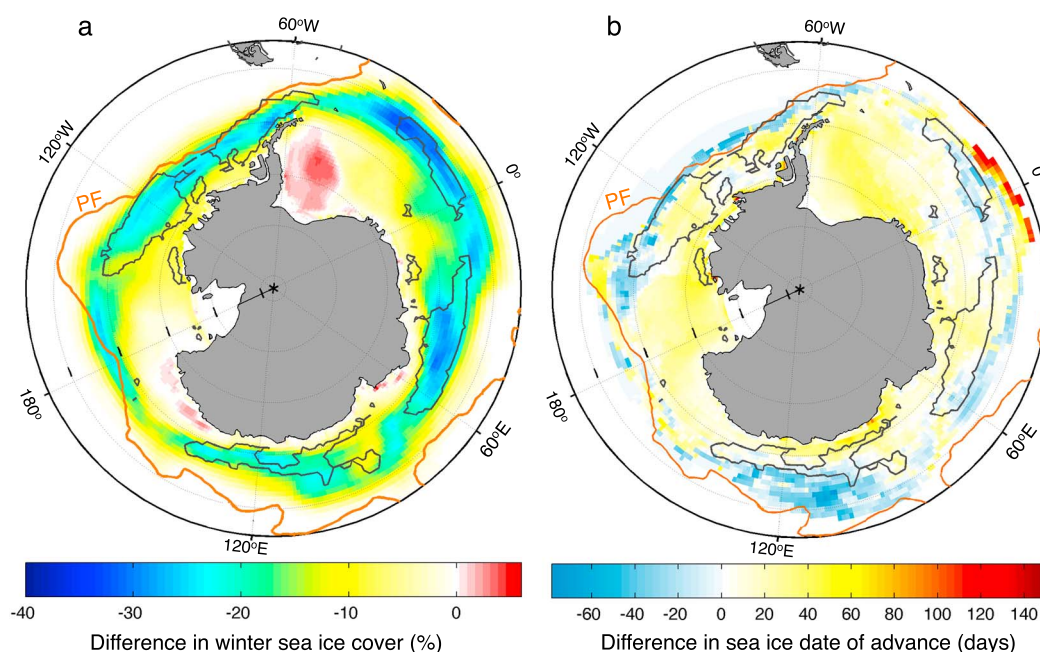


Figure 3. Projected changes in (a) winter sea ice cover (expressed as percentage (%) of sea ice cover) and (b) sea ice date of formation (days) by the end of the 21st century. Generally, negative changes in Figure 3a indicate a loss of sea ice while positive changes in Figure 3b indicate a delay in the time of winter sea ice formation. The black contours south of the Polar Front (PF) show regions where more than 12 climate models agree with the sign of mean sea ice distribution change (see supporting information).

Predictions of the winter sea ice distribution for the end of the 21st century show a 30–35% decrease in sea ice extent around the edges of the marginal sea ice along the eastern Weddell Sea toward King Haakon VII Sea, extending to the southwest of the Kerguelen Plateau. Sea ice extent decreases by 20–30% along the entire western Antarctic Peninsula and in the areas close to the continental shelf off Wilkes Land (Figure 3a). Within these regions sea ice seasonal duration decreases by 30–40 days (Figure 3b). We find that the regions experiencing the strongest decline in sea ice extent and duration are consistent with the modeled areas that support successful krill spawning under present-day conditions. In turn, successful spawning distributions are consistent with the observed krill distributions (e.g., Figure 2e), while projected sea ice reductions and changes in time formation may negatively influence recruitment success in these regions by the end of the century.

Future projections suggest a 51% overall decline in the area of the krill spawning habitat, assuming reduced sea ice cover and decreased chlorophyll *a* availability by 25% (Figure 4a, regions in orange). When only the regions where 12 or more models agree with sea ice reduction, this decline is 41%. Recent modeling efforts, however, predict a decrease of 51% in the global chlorophyll *a* concentration by 2100 [Olonscheck *et al.*, 2013]. When we halve summer chlorophyll *a*, the krill habitat shrinks by 83% (all habitat) and 71% (projected regions where 12 or more models agree) (Figure 4b). Krill habitat along the western Antarctic Peninsula north of Marguerite Bay completely disappears. The regions most affected are the northern Weddell Sea and the eastern Ross Sea, where the spawning habitat extension is reduced to regions south of 63°S. Other observational studies examined the effects of primary productivity in the Southern Ocean—9 years of satellite observations did not present a trend in annual primary production estimated from Chlorophyll *a* [Arrigo *et al.*, 2008]. When we maintain present-day chlorophyll *a* availability, the habitat is reduced by 13% (Figure 4d). Further modeling studies predict an increase in net primary production (NPP) around the Southern Ocean [Bopp *et al.*, 2013; Boyd *et al.*, 2015]. Our simulations using a 25% increase of present-day chlorophyll *a* improve krill's habitat by 43% (all habitat) and 46% (projected habitat where 12 or more models agree) but mostly in regions that at present day support krill's growth (Figure 4e). When we use sea ice trends from the observations and chlorophyll *a* is reduced by 25%, only the southern Antarctic Peninsula toward the Bellingshausen Sea supports krill spawning (Figure 4c). If chlorophyll *a* increases by 25% the regions off King Haakon VII Sea, east of Prydz Bay, Amundsen Sea, and around South Orkney Islands support krill's survival (Figure 4f).

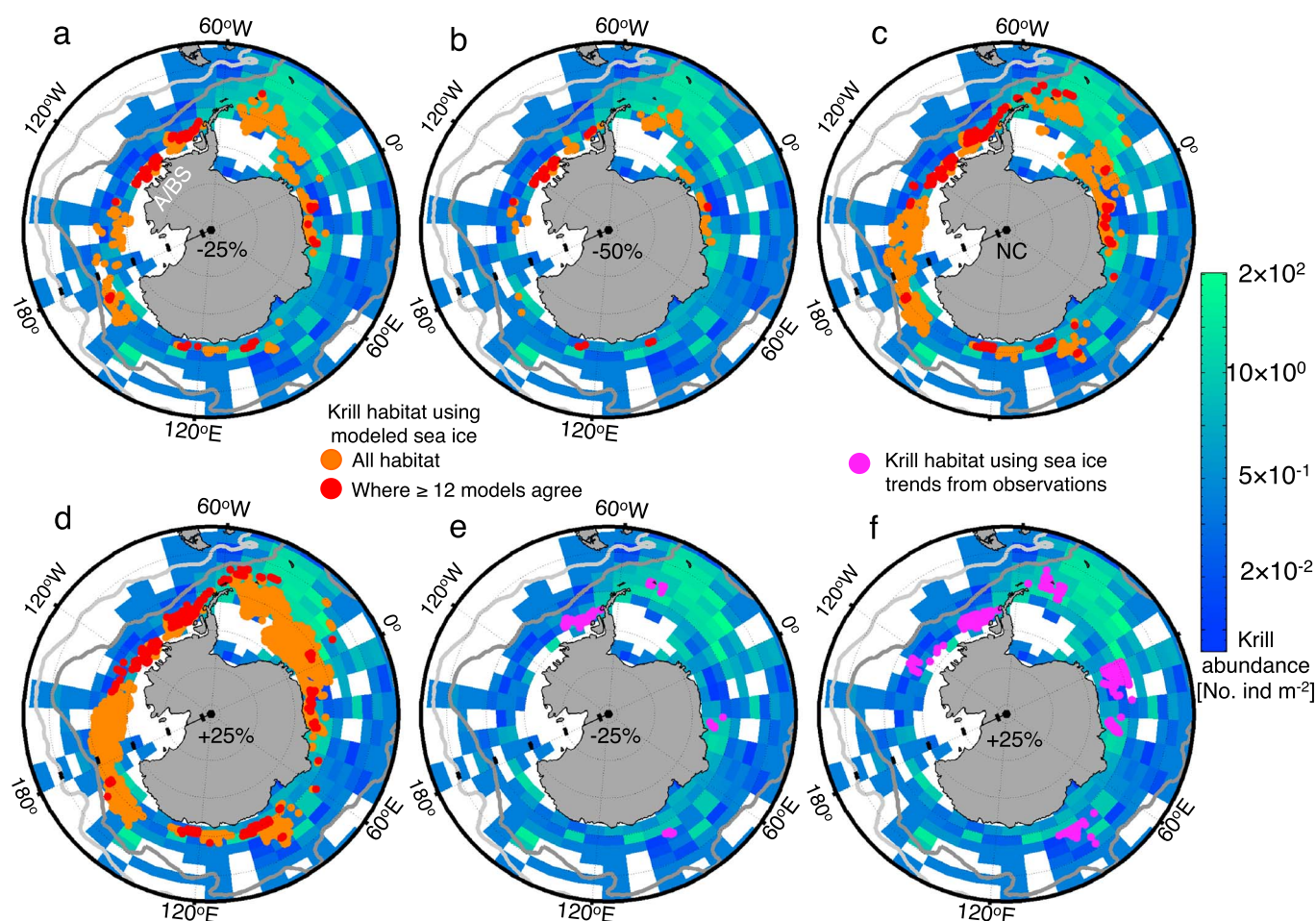


Figure 4. Circumpolar projections of krill spawning habitat at the end of the 21st century under business as usual CO₂ emissions. These projections incorporate the effects of increased ocean temperature, modeled sea ice reduction, and chlorophyll *a* (Chl *a*) decline, for (a) 25% and (b) 50% reduction as well as (c) no change (NC) and (d) 25% increase of the chlorophyll *a* concentration with respect to present-day observations. Projected krill habitat within regions where modeled sea ice agree with the sign of the mean (e.g., Figure 3) is shown in red, projected krill habitat outside this region is shown in orange. Two panels on the right show krill habitat (magenta) obtained using sea ice trends from observations and chlorophyll *a* decline of (e) 25% and increase of (f) 25% from present day concentrations. The blue-green colored map gives the circumpolar distribution of krill adults in historical observations (as in Figure 4 from Atkinson *et al.* [2008]). The Amundsen/Bellingshausen Sea regions are marked (A/BS).

4. Discussion

Our results suggest that by the year 2100, a combination of several factors including the reduced sea ice cover, the delayed timing of sea ice advance, and the lesser availability of chlorophyll *a* will alter the reproductive output of krill, hindering the survival of larvae, with detrimental consequences for marine mammals and seabirds who obtain most of their required energy from krill [Forcada *et al.*, 2008; Schofield *et al.*, 2010; Ballerini *et al.*, 2014; Hill *et al.*, 2012, 2013]. The descent-ascent model itself shows early hatching and faster development which increase the survival of the larvae during winter, because they enter the winter season at a more advanced stage with sufficiently high lipid reserves [Pakhomov *et al.*, 2004; Meyer *et al.*, 2009]. However, even though increasing ocean temperatures accelerate larval development, they also exert physiological stress and affect krill's metabolic processes. Previous studies have shown that rising ocean temperatures can alter the molt rates and growth of krill juveniles and adults—these rates are optimal at 2°C but decline at higher and lower temperatures [Atkinson *et al.*, 2006; Tarling *et al.*, 2006]. For krill larvae the physiological consequences of rising ocean temperature above 2°C has yet to be determined, but from these studies on krill adults we could extrapolate similar consequences, such that increasing ocean temperatures could place the larvae under suboptimal conditions close to the limits of their physiological tolerance. This and other factors discussed below may negate any potential benefits for krill development.

Projections for the krill habitat under low chlorophyll *a* availability suggest that krill spawning will persist only in limited areas of the western Weddell Sea (Figures 4a and 4b), isolated areas along the Indian sector and the Amundsen/western Bellingshausen Sea. At present, this last region does not support successful krill spawning (e.g., Figure 2e), but it might open up as a potential new habitat. A delay in sea ice formation and smaller sea ice cover would increase the number of ice-free summer days, boosting light availability, which could translate into a higher phytoplankton growth [Montes-Hugo *et al.*, 2009] and potentially facilitate the survival of krill larvae, leading to a higher krill recruitment success [Quetin and Ross, 2003] and increasing their population size in the Amundsen/Bellingshausen Seas area. However, it is debatable that this new habitat, which occupies less than one fourth of the present day habitat of the wAP and southwest Atlantic sector, will be sufficient to maintain current krill stocks downstream along the southwest Atlantic sector and South Georgia and/or to support all the krill-dependent predators. Temperature-food interactions (ocean temperature-chlorophyll) over the 21st century are also likely to affect the habitat's ability to support postlarval krill growth in the Weddell Sea with major repercussions for predators that forage from breeding sites on South Georgia [Hill *et al.*, 2013].

The simulated krill habitat in 2100 shrinks by ~80% when chlorophyll *a* is reduced to half of the present-day values. The complete disappearance of spawning grounds along the west Antarctic Peninsula is one of the most dramatic results. This area is widely recognized as the main seeding region for krill adults residing in the southwest Atlantic sector [Hofmann *et al.*, 1992; Fach *et al.*, 2002, 2006; Thorpe *et al.*, 2004, 2007], where 70% of the present-day krill stock is concentrated [Atkinson *et al.*, 2008]. Lagrangian tracking experiments show that about one third of the simulated larvae spawned along the shelf break and more than two thirds of the juvenile krill produced on the continental shelf of the wAP are transported toward the north of the Antarctic Peninsula [Piñones *et al.*, 2013] and eventually are recruited into the populations of the Scotia Sea and South Georgia regions [Fach *et al.*, 2002; Thorpe *et al.*, 2007]. A sensitivity study focusing on the strengthening of winds and the Antarctic Circumpolar Current (ACC) transport along wAP [Dinniman *et al.*, 2012] has shown winter sea ice reductions consistent with the reductions along wAP projected for 2100, which also agrees with the observed regional decline in sea ice extent of the last 40 years [Stammerjohn *et al.*, 2008].

Recent modeling efforts show a projected increase in net primary production (NPP) around the Southern Ocean [Bopp *et al.*, 2013]. Boyd *et al.* [2015] suggest an interplay of multistressors for this area, where regional variations do not necessarily match the expectation from global trends (decrease in NPP). Together, the warming and higher iron supply would increase diatom growth rates [Rose *et al.*, 2009] and enhance net primary production driven by higher CO₂ concentrations. These authors also raise the point that it is difficult to make a prediction of phytoplankton response to multistressors and at present not yet possible. Studies of the tendency of chlorophyll *a* concentrations obtained from satellite observations suggest a decrease of 10.4% in primary production between the 1990s and the 1980s for the Southern Ocean [Gregg *et al.*, 2003], but no trend is observed in primary production in a 9 year time series calculated from remotely sensed ocean color, sea surface temperature, and sea ice concentration [Arrigo *et al.*, 2008]. Using sea ice from climate models and observed sea ice trends under multiple scenarios for chlorophyll *a* concentrations provide different projections for the habitat of krill at the end of the century (e.g., Figure 4). When sea ice obtained from climate models is used, the simulated krill habitat expands by 43% if chlorophyll *a* increases by 25% (Figure 4d), opposite to what was observed when sea ice from climate trends is used under similar chlorophyll *a* increase (Figure 4f). The 43% expansion in the habitat is primarily in the regions where present-day conditions support krill growth and the largest abundances are observed [e.g., Atkinson *et al.*, 2008]. However, an increase in chlorophyll *a* not necessarily assures an expansion of the krill habitat (i.e., Figure 4f). When sea ice trends from observations are used, even under increased chlorophyll *a* (25% increase) availability the projected krill habitat is limited to small regions along the Bellingshausen Sea, western Antarctic Peninsula, western Weddell Sea and King Haakon VII Sea. When chlorophyll *a* is maintained at present-day levels the habitat declines by 13% (e.g., Figure 4c). Under this last scenario, the change in sea ice date of formation is responsible for such decline, affecting directly krill's recruitment that defines survival during the third critical period [Quetin *et al.*, 2007]. A recent study of the effects of climate change on krill adult growth in the Weddell Sea [Hill *et al.*, 2013] suggest potential negative effects such that the projected warming could reduce krill's growth and affect egg production. A reduction in krill availability would produce a decline in the air-breathing predator populations at South Georgia. These changes would still cause degradation of the habitat even if available chlorophyll *a* concentration were to increase by 50%.

Thus, the large uncertainties in the CMIP5 sea ice extent and formation provide uncertainties in our projections for the krill habitat; changes in krill habitat in regions with higher robustness in our projections are the wAP and the Amundsen and Bellingshausen Seas. Thus, along the wAP the fate of Antarctic krill may be controlled by the large changes in sea ice advance, in particular, for the region north of Marguerite Bay, despite increases in available chlorophyll *a*. The Amundsen and Bellingshausen Seas may become new seeding regions providing larvae for krill populations residing downstream (e.g., North Antarctic Peninsula, Weddell and Scotia Seas).

The aforementioned impacts add to the effect of other environmental factors that could potentially reduce krill population abundance but have not been accounted for in this study, such as the ongoing ocean acidification [Kawaguchi *et al.*, 2013]. Experiments exposing krill eggs to elevated seawater CO₂ levels [Kawaguchi *et al.*, 2013] provided projections of the threat of ocean acidification, which becomes especially alarming by the year 2300 with an 80–90% reduction in krill egg hatching rate. Kawaguchi *et al.* [2013] showed that hatching rate is mildly reduced (20%) by 2100 in most of the Southern Ocean; only localized areas around Weddell Sea and the Haakon VII Sea show hatching rates reductions of 60–70%. Our results go a step forward in predicting the fate of krill, since our projections include the combined effects of rising ocean temperatures, the reduction of sea ice cover, changes in the timing of sea ice advance, and reduced chlorophyll *a* availability, providing a circumpolar view of the regions that will be affected the most. An 80% contraction of the available krill spawning habitat under the business-as-usual emission scenarios raises serious concerns on the potential threats to the Antarctic marine food web and the fate krill fisheries might face later in this century. Krill stock is already experiencing a long-term decline [Atkinson *et al.*, 2008], despite being currently underexploited [Food and Agriculture Organization of the United Nations, 2005; Hill, 2013]. Any further disruption of the krill habitat will have major implications for Antarctic ecosystems with significant commercial repercussions.

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