Abstract
Antarctic krill is an obligate cold water species, an increasingly important fishery resource and a major prey item for many fish, birds and mammals in the Southern Ocean. The fishery and the summer foraging sites of many of these predators are concentrated between 0° and 90°W. Parts of this sector have experienced recent localised sea surface warming of up to 0.2°C per decade, and projections suggest that further widespread warming of 0.27° to 1.08°C will occur by the late 21st century. We used a statistical model linking Antarctic krill growth to temperature and chlorophyll concentration to assess the influence of projected warming on Antarctic krill habitat quality. The results divide the sector into two zones: A band around the Antarctic Circumpolar Current in which habitat quality is particularly vulnerable to warming; and a southern area which is relatively insensitive. Our analysis suggests that the direct effects of warming could reduce the area of growth habitat by up to 20%. The reduction in growth habitat within the range of predators, such as Antarctic fur seals, foraging from breeding sites on South Georgia could be up to 55%, and the habitat's ability to support Antarctic krill biomass production within this range could be reduced by up to 68%. Sensitivity analysis suggests that a 50% change in summer chlorophyll concentration could have a more significant effect on Antarctic krill habitat than the direct effects of warming. A reduction in primary production could lead to further habitat degradation but even a 50% increase in chlorophyll would not completely negate the degradation of habitat available to predators. While there is considerable uncertainty in these projections, they provide strong and specific evidence that climate change poses a threat to Antarctic krill growth habitat and consequently to Southern Ocean biodiversity and ecosystem services.

POTENTIAL CLIMATE CHANGE EFFECTS ON THE HABITAT OF ANTARCTIC KRILL

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ABSTRACT

Antarctic krill is an obligate cold water species, an increasingly important fishery resource and a major prey item for many fish, birds and mammals in the Southern Ocean. The fishery and the summer foraging sites of many of these predators are concentrated between 0° and 90°W. Parts of this sector have experienced recent localised sea surface warming of up to 0.2°C per decade, and projections suggest that further widespread warming of 0.27° to 1.08°C will occur by the late 21st century. We used a statistical model linking Antarctic krill growth to temperature and chlorophyll concentration to assess the influence of projected warming on Antarctic krill habitat quality. The results divide the sector into two zones: A band around the Antarctic Circumpolar Current in which habitat quality is particularly vulnerable to warming; and a southern area which is relatively insensitive. Our analysis suggests that the direct effects of warming could reduce the area of growth habitat by up to 20%. The reduction in growth habitat within the range of predators, such as Antarctic fur seals, foraging from breeding sites on South Georgia could be up to 55%, and the habitat's ability to support Antarctic krill biomass production within this range could be reduced by up to 68%. Sensitivity analysis suggests that a 50% change in summer chlorophyll concentration could have a more significant effect on Antarctic krill habitat than the direct effects of warming. A reduction in primary production could lead to further habitat degradation but even a 50% increase in chlorophyll would not completely negate the degradation of habitat available to predators. While there is considerable uncertainty in these projections, they provide strong and specific evidence that climate change poses a threat to Antarctic krill growth habitat and consequently to Southern Ocean biodiversity and ecosystem services.

INTRODUCTION

Climate warming is already producing complex spatial and seasonal changes in the Earth's habitats and ecosystems (Parmesan & Yohe 2003, Burrows et al. 2012). Warming is expected to increase significantly over the 21st Century (IPCC 2007) leading to ecosystem change and potentially severe socioeconomic consequences (Cheung et al. 2009). Observed changes in the Southern Ocean include localised sea ice loss (Stammerjohn et al. 2009) and increases in summer sea surface temperatures (SSTs) of 1°C over 5 decades near the western coast of the Antarctic Peninsula (Meredith & King 2005) and 0.9°C over 8 decades at South Georgia (Whitehouse et al. 2008). Previous studies have suggested critical relationships between climate-related variables (sea temperature, ice cover and pH) and the recruitment, survival, growth and distribution of crustacean Antarctic krill, *Euphausia superba* (Atkinson et al 2004 Quetin et al 2007, Kawaguchi et al. 2011). Antarctic krill is a characteristic species of the Southern Ocean which exists within a narrow band of cold temperatures (up to ~5°C) (Marr 1962, Atkinson et al. 2008, Mackey et al 2012). It is an increasingly important fishery resource and a major prey item for a diverse suite of predators including whales, penguins, seals and fish (Marr 1962, Atkinson et al 2001, Hill et al 2012). Further environmental changes are likely to affect Antarctic krill and consequently the biodiversity and ecosystem services of the Southern Ocean.

Antarctic krill has an estimated circumpolar biomass >2×10^8t, about one-quarter of which is concentrated in about 10% of its total habitat area, specifically the Scotia Sea and Southern Drake passage (Fig. 1) (Marr 1962, Atkinson et al 2008; 2009; 2012; Hill 2013). This is also where the majority of Antarctic krill fishing has occurred and where many air breathing vertebrates congregate to feed on Antarctic krill and rear offspring on islands such as South Georgia (Murphy et al. 2007, Hill 2013). About 95%, 50% and 25% (Kovacs & Lowry 2008 Butchart & Taylor 2012,a,b) of the global populations of Antarctic fur seals, (*Arctocephalus gazella*), grey headed albatrosses (*Thalassarche chrysostoma*) and wandering albatrosses (*Diomedea exulans*) breed at South Georgia where Antarctic krill constitute approximately 85%, 76% and 12% of their respective diets (Hill et al 2012, Xavier et al 2003).

The role of Antarctic krill in supporting predators might be more significant than that of any comparable species elsewhere in the world (Pikitch et al 2012). It is also an abundant fishery resource which, according to the Food and Agriculture Organisation of the United Nations, is underexploited (FAO 2005). It has a potential harvest exceeding 10% of current global marine

fisheries production (Nicol et al 2012, FAO 2012). It is therefore important to evaluate the potential effects of climate change on Antarctic krill.

In this study, we examine some of these effects by assessing potential changes in the habitat's ability to support growth. Growth represents the accumulation of resources within an individual or population and is therefore a valuable indicator of overall habitat quality (Pörtner 2012). Growth also underpins biomass production and its availability to predators and fisheries. The growth of Antarctic krill can be equivalent to a four-fold annual increase in individual mass under optimal conditions (Atkinson et al. 2009). We use a statistical model linking Antarctic krill growth to body size, SST and food availability (Atkinson et al 2006) with projected SST changes from the Coupled Model Intercomparison Project Phase 5 multi-model ensemble (Taylor et al 2012) to assess potential changes in Antarctic krill growth habitat by the late 21st century. We focus on the 90° longitudinal sector that encompasses the Scotia Sea and Southern Drake passage, and we assess the effects on habitat within the foraging ranges of predators at South Georgia in more detail.

METHODS

Models and metrics

An assessment of various models for evaluating Antarctic krill growth habitat on the basis of temperature concluded that only one of the available models has sufficient empirical support (Wiedenmann et al. 2008). This is a statistical model derived from observed growth rates of Antarctic krill caught in a wide range of environmental conditions (Atkinson et al 2006). The model relates the daily increase in Antarctic krill length (daily growth rate: *DGR*, mm d^{-1}) to sea surface temperature (*SST*, °C), food availability indicated by chlorophyll-a concentration (*CHL*, mg m^{-3}), and starting length (*L*, mm):

$$DGR = -0.066 + 0.002L - 0.000061L^2 + \frac{0.385CHL}{0.328+CHL} + 0.0078SST - 0.0101SST^2 \quad (1)$$

The following relationship which, was derived from the same data as equation 1 (Atkinson et al 2006), converts individual Antarctic krill length to dry mass, *M* (g):

$$\log_{10}(M) = 3.89\log_{10}(L) - 4.19 \qquad (2)$$

A previous study (Atkinson et al 2009) used equations 1 and 2 to estimate Gross Growth Potential (GGP) based on spatially resolved, monthly averages of *SST* and *CHL*. GGP is the model-predicted dry mass of an individual Antarctic krill at the end of the summer growth season divided by dry mass at the beginning of the season, and is thus a unitless quantity that indicates the habitat's ability to support Antarctic krill growth.

We used this approach to estimate the effects on GGP of projected SST changes by the late 21st century. We used equation 1 to calculate the length increase per week based on monthly averaged environmental data. For weeks that straddled two months, we used weighted averages of the environmental data from those two months. We updated the Antarctic krill starting length at the beginning of each week and converted the initial and final lengths to dry mass using equation 2. Finally we divided final mass by starting mass to estimate GGP.

The CMIP5 dataset (Taylor et al., 2012) provides the results of climate simulations conducted with multiple climate models. Simulations to 2005 were run with observed variations of important factors such as greenhouse gases and aerosols. Simulations from 2006 were forced with Representative Concentration Pathways (RCPs), which include representations of changes to factors such as greenhouse gas and air pollutant emissions and land-use, and are named according to radiative forcing in the year 2100 (van Vuuren et al 2011). RCP2.6 has peak radiative forcing of ~3 W m^{-2} in the first half of the 21st century, falling to ~2.6 W m^{-2} by 2100. In this scenario, aggressive mitigation results in negative net greenhouse gas emissions by the end of the century. Under RCP4.5, greenhouse gas emissions rise until around 2040 before falling below those for the year 2000 by the end of the century, and radiative forcing stabilizes at ~4.5 W m^{-2} around 2100. Under RCP8.5, radiative forcing reaches 8.5Wm^{-2} in 2100 and continues to rise (Taylor et al. 2012,van Vuuren et al 2011).

We used results from RCP2.6, RCP4.5 and RCP8.5 to calculate projected 21st Century SST changes for the Southern Ocean in the longitudinal sector 0°W to 90°W. We define the Southern Ocean as the marine area south of the Antarctic Polar Front (position defined in Orsi et al 1995, 2008 update available from:
https://data.aad.gov.au/aadc/metadata/metadata_redirect.cfm?md=/AMD/AU/southern_ocean_fronts). We also explored the implications for GGP of projected SST change in the same sector for the area south of 50°S (the study area). 50°S is the northern limit of Antarctic krill distribution (Marr 1962, Atkinson et al 2008).

To estimate current GGP, we used monthly estimates of current SST based on observations (Feldman & McClain 2007a)which we label $SST_{o,m,c}$. Subscript o indicates that the data are observations, m indicates the month and c indicates that the estimate is a climatology (i.e. a long term average). Climatological estimates are appropriate for variables such as SST which have high interannual variability (Stock et al 2011). Our estimates of projected GGP were based on estimates of projected SST, $SST_{p,m,y}$, from the CMIP5 results, where the subscript p indicates that the data are projections and y indicates year. To correct for bias in model estimates of SST (Stock et al 2011), we converted projected SST into differences from an SST climatology for the same model representing current conditions, $SST_{b,m,c}$, and added the current climatology based on observations, $SST_{o,m,c}$, to calculate a bias-corrected SST estimate, $SST'_{p,m,y}$:

$$SST'_{p,m,y} = SST_{p,m,y} - SST_{b,m,c} + SST_{o,m,c} \tag{3}$$

We used this bias-corrected SST estimate to calculate projected GGP.

The World Meteorological Organisation recommends calculating average conditions over 30 years (http://www.wmo.int/pages/prog/wcp/ccl/faqs.html). We therefore selected the period 1991-2020 for $SST_{b,m,c}$ and we obtained $SST_{p,m,y}$ for each year 2070-2099. The climatological period for $SST_{o,m,c}$ was restricted by data availability to 1998 – 2010. We obtained $SST_{b,m,c}$ and $SST_{p,m,y}$ for each available model in the CMIP5 results. Within each RCP, SST estimates for each model were calculated as the mean of the estimates for all realisations available for that model. Consequently contributions from all models were given equal weight in across-model means, regardless of the number of realisations per model. In addition to SST data, GGP estimation requires a starting length and *CHL* estimates. We used a starting length of 40mm, which is the observed mean length for the postlarval population (Atkinson et al 2009). We used remote-sensed, spatially-resolved *CHL* estimates ($CHL_{o,m,c}$) (Feldman & McClain 2007b). The climatological period for $CHL_{o,m,c}$ was restricted by data availability to 1997 – 2010. We also varied these *CHL* estimates to assess the sensitivity of our results to assumptions about chlorophyll-a concentration. One study estimates that the Southern Ocean experienced a 10% decline in chlorophyll-a concentration over the 1980s and 1990s (Gregg et al. 2003). We linearly extrapolated this change over nine decades and therefore increased and decreased the *CHL* estimates by 50%. We were thus able to calculate spatially-resolved estimates of current GGP using $SST_{o,m,c}$ and $CHL_{o,m,c}$, and estimates of projected GGP for each year 2070-2099 for each relevant CMIP5 model, and each of three RCPs.

Our GGP estimates for the period 2070-2099 were resolved to grid cell (1° longitude by 0.5° latitude), model and projection year. We averaged across years and models to derive a single estimate of projected GGP for each combination of grid cell, chlorophyll-a concentration, and RCP. We then subtracted the **estimated current GGP** (i.e. that calculated using observed SSTs, $SST_{o,m,c}$, and observed **chlorophyll-a concentrations,** $CHL_{o,m,c}$) from projected GGP to estimate the **GGP change** between the current period and 2070-2099.

From our spatially-resolved GGP estimates, we calculated three spatially-aggregated metrics for each combination of chlorophyll-a concentration and RCP: (1) average GGP by year; (2) total GGP; and (3) growth area. Average GGP by year is the mean of across-model, grid-cell-and-year-specific GGP estimates where they were ≥1. GGP<1 is an indicator of nonviable habitat. It implies shrinkage resulting from starvation, which and has been observed in Antarctic (Nicol et al. 1992). To estimate total GGP we first calculated, for each grid cell in each model, the across-year mean GGP for the period 2070-2099. We then calculated, for each model, the area-weighted sum of those resulting grid cell-specific estimates of GGP that were ≥1. Total GGP is the across-model mean of this sum. Weighting by grid cell area was necessary because this area changes with latitude. To estimate growth area we calculated, for each model, the total area of all grid cells in which the across-year mean GGP was ≥1. Growth area was the across-model mean of this sum.

We estimated projected change relative to current conditions in the form of **relative GGP** and **relative growth area**. We calculated these relative values by dividing total GGP and growth area by the equivalent metric calculated using observed SSTs, $SST_{o,m,c}$, and **chlorophyll-a concentrations,** $CHL_{o,m,c}$. Our estimate of relative GGP excludes GGP values <1 and therefore does not include further degradation of already nonviable habitat but it does include previously hostile habitat becoming viable for growth. We calculated relative GGP and relative growth area both for our entire study area, and within the foraging ranges of representative Antarctic krill predators at South Georgia.

Data

We obtained spatially-resolved monthly mean SST data at a nominal horizontal resolution of 9km for the austral summer periods (December to March) from December 2002 to March 2011 from the archive of Aqua MODIS level 3 data (Feldman GC, McClain 2007a), and chlorophyll-a concentration

data for the austral summer periods from December 1997 to March 2010 from the archive of SeaWIFS data (Feldman GC, McClain 2007b) . Both of these datasets are available through the NASA OceanColor website (*oceancolor.gsfc.nasa.gov*). We obtained spatially-resolved, monthly mean SST data for the period 1990 – 2100, for each relevant RCP, from the output of up to 16 climate models which are available as part of the CMIP5 multi-model ensemble results (Taylor et al. 2012). The CMIP5 model data were downloaded from the distributed CMIP5 archive accessed via the Program for Climate Model Diagnosis and Intercomparison CMIP5 data portal (http://cmip-pcmdi.llnl.gov/cmip5/data_portal.html). We used all relevant results that were available on 31 Jan 2012 (Table 1).

In addition to analysing habitat quality across the study area, we also extracted statistics for the areas within each of three concentric distances from South Georgia that indicate the foraging ranges of representative near, medium and long-range foragers. These distances were 140 km, 610 km, and 1200 km which respectively indicate the foraging ranges of Antarctic fur seals (Staniland Boyd 2003); wandering albatrosses (Xavier et al 2003) and grey headed albatrosses (Xavier et al 2003) during offspring rearing.

All the data were processed onto a common grid of 1° longitude by 0.5° latitude. The boundaries of these cells were also the outer boundaries of the constituent remote-sensed SST and chlorophyll-a concentration data, so for these data we simply calculated the mean of the 72 constituent data points. Some of the CMIP5 SST data were provided on a regular grid. We sampled these data onto the 1° by 0.5° grid using bilinear interpolation (Press et al 1992). For data not provided on a regular grid, all grid points were used to generate a Delaunay triangulation (Lee & Schachter 1980) on an equirectangular projection, and the data were sampled from this triangulation onto the 1° by 0.5° grid by linear interpolation (Coxeter 1969). Grid points whose interpolated value was affected by a land point were flagged as missing data. This means that GGP estimates in coastal cells are informed by varying numbers of models. However, this does not affect any of our main conclusions.

The availability of remote-sensed SST and chlorophyll-a concentration data varies temporally due to the presence of cloud and ice cover. This variability is reflected in the available monthly mean data products where cells with insufficient coverage appear as missing data. Our objective was to achieve extensive spatial coverage with sufficient observations in each cell to provide representative monthly SST and chlorophyll-a concentration estimates for the summer growth season. A suitable balance of spatial and temporal coverage was achieved by including only those 1° by 0.5° cells with a minimum of 20% spatial data coverage per month for at least 3 years during the climatology period.

To maximise spatial data coverage, we constructed the climatologies from the full period of data availability for each data type separately, and restricted the analysis to the period January to March. The majority of krill growth occurs between December and March (Marr 1962), and a previous study of current habitat quality used this four month period (Atkinson et al 2009) but consequently had less spatial coverage. The application of these criteria defined the areas for inclusion and exclusion of data in our calculations, which we applied consistently to each model and observation based data set that we used.

RESULTS

The growth model correctly identifies the warmer waters north of the Antarctic Polar Front as unable to support krill growth (Fig. 2). Current GGP in the study area shows considerable spatial structure with patches of elevated habitat quality along the coast of the Antarctic continent, and around the South Orkney and South Sandwich islands. These patterns were less distinct but still apparent with changed chlorophyll-a concentrations. The masked areas in the southern Weddell Sea and along the coast of the Antarctic Peninsula had low data availability due to frequent ice cover.

Monthly climatological SSTs from CMIP5 models for the period 1991-2020 were, on average, 2.04°C warmer than SST estimates for 2002-2011 from Aqua MODIS data, but there was reasonable correlation between the two datasets (r=0.954). The mean projected summer SST warming for the area south of the Antarctic Polar Front between 1991-2020 and 2070-2099 was 0.27°C, 0.56°C and 1.08°C for RCP2.6, RCP4.5 and RCP8.5 respectively. These estimates varied between years and between models (Fig. 3).

Projected GGP losses were concentrated in a band that approximates the location of the ACC (Fig. 4). Most models projected significant warming of the ACC under RCP4.5 and RCP8.5. The RCP2.6 results identified an area of warming in the west Scotia Sea, but otherwise there was little concordance amongst RCP2.6 results about projected changes in GGP. In the areas where ≥90% of model projections agreed on the sign of change in GGP, the projected GGP declines (with unchanged chlorophyll-a concentrations) were 16%, 25% and 37% for RCP2.6, RCP4.5 and RCP8.5 respectively. The corresponding reductions in growth area were 13%, 23% and 33%. The projections included moderate gains in habitat quality on the continental coast in the far west of the study area, but <90% of model projections agreed on the sign of change in GGP for much of this area.

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The projected GGP declines (with unchanged chlorophyll-a concentrations) were 7%, 12% and 22% for RCP2.6, RCP4.5 and RCP8.5 respectively (Fig. 5). The corresponding reductions in Antarctic krill growth area were 5%, 10% and 20% for RCP2.6, RCP4.5 and RCP8.5 respectively. Inevitably a 50% reduction in chlorophyll concentration led to greater reductions in both GGP and growth area. When chlorophyll-a concentration was increased by 50%, the projected warming under RCPs 4.5 and 8.5 still led to significant reductions in growth area. Nonetheless, the effect of a 50% increase in chlorophyll-a concentration was sufficient to offset the overall effects of warming on relative GGP.

South Georgia is located in the band of projected habitat loss. Consequently there were pronounced negative effects within the foraging ranges of predators breeding on this island. These negative effects were greatest for those predators with the most restricted foraging ranges (Fig. 6), where the projected GGP declines (with unchanged chlorophyll-a concentrations) were 9%, 24% and 68% and the corresponding reductions in growth area were 5%, 6% and 55% for RCP2.6, RCP4.5 and RCP8.5. Even the combination of the long foraging range of grey headed albatrosses and an increase in chlorophyll-a concentration was not sufficient to prevent the negative effects projected for RCP8.5.

DISCUSSION

The projected effects of plausible SST warming on Antarctic krill growth habitat are mainly negative. Under all RCPs that we considered, the projections imply a decrease in habitat quality over the 21st century, particularly in the ACC. Our analysis suggests that these effects could be offset to some extent if warming leads to an overall increase in chlorophyll production. Habitat quality could improve in some marine areas close to the Antarctic continent even under the most extreme warming scenario. However this does not seem sufficient to offset the negative impacts within the foraging ranges of birds and seals breeding at South Georgia.

Recent SST warming rates at South Georgia and the western Antarctic Peninsula (Meredith & King 2005, Whitehouse et al. 2008) are in the upper range of projected regional warming rates for the 21st century. However, some parts of the Southern Ocean have cooled over recent decades and experienced associated increases in sea ice (Parkinson et al. 2004). Previous modelling studies suggest that recent warming might have already degraded Antarctic krill habitat in some areas (Wiedenmann et al. 2008, Mackey et al 2012). A study using the growth model used here concluded that, for the period 1970-2004, increasing temperatures probably reduced lifetime biomass production of Antarctic krill at South Georgia but increased it at the Antarctic Peninsula

(Wiedenmann et al. 2008). Our results suggest that, in the future, increasing temperature could reduce growth in both of these areas.

Climate affects species through their habitats. Understanding these habitat effects is a prerequisite for understanding effects on biological variables such as abundance and biomass production. There are many routes through which changing habitats can influence these variables. For example, successful completion of the Antarctic krill life cycle apparently requires spawning in water with specific depth and temperature characteristics (Marr 1962, Hofman and Hüsrevoğlu 2002) and larval development under sea ice (Quetin et al 2007). Winter processes are also important in dictating habitat suitability for adults, but the summer months that we model encompass their main growth period. Other environmental variables, such as pH, might also be critical for the sensitive larval stages (Kawaguchi et al. 2011). Furthermore, the distribution of Antarctic krill seems to be affected by ocean currents which may transport individuals thousands of kilometres in a lifetime (Thorpe et al. 2007). Thus, high quality growth habitat will only result in high biomass production if sufficient Antarctic krill arrive in the area as a result of transport or local spawning.

These multiple environmental influences on Antarctic krill abundance and biomass production have several implications. Firstly, more detailed mechanistic life-cycle and population models are needed to better assess the potential effects of climate change (Quetin et al 2007, Stock et al. 2011). Secondly, these effects are likely to be more complex than a simple poleward shift in distribution. Some of the oceanographic characteristics on which Antarctic krill rely, such as the deep waters of the ACC, will not migrate south as the ocean warms. While coastal embayments and high latitude shelves may be reasonable refugia for growth, they are unlikely to provide appropriate habitats for spawning (Hofman and Hüsrevoğlu 2002) or connecting subpopulations (Siegel 2005).

Large scale analyses of ecological responses to climate change generally stress the effects of warming (Parmesan and Yohe, Burrows et al. 2011). Polar studies also tend to emphasise warming because polar organisms are sensitive to temperature (Pörtner and Farrel 2008, Peck et al. 2004), which is rising rapidly in some polar regions (Meredith and King 2005, Steele et al 2010). Nonetheless, food availability is also an important habitat characteristic which, at the physiological level, can sometimes compensate for the negative effects of temperature (Pörtner 2012). This is illustrated by the high Antarctic krill abundances and growth rates found at South Georgia. This is near the northern limit of the species' range and has relatively high and physiologically stressful temperatures, but it also has very high food concentrations (Fig. 1, Atkinson et al. 2008). Temperature-food interactions are therefore likely to influence the ecological effects of climate

change (Pörtner 2012), and using models, such as ours, that explicitly include the effects of food availability is a useful step towards fuller consideration of the multiple interacting effects of climate change (Stock et al. 2011).

Previous studies have reported a 10% decline in chlorophyll-a concentration in the Southern Ocean over the 1980s and 1990s (Gregg et al. 2003) and substantial localised increases and decreases in chlorophyll-a concentration at the Antarctic Peninsula in the last 30 years (Montes-Hugo et al 2009). Such changes are associated with changes in the composition of the phytoplankton community. The main effects at the Antarctic Peninsula were an overall decline in chlorophyll-a concentration and a decrease in the abundance of diatoms relative to other phytoplankton (Moline et al. 2004, Montes Huugo et al. 2009). Such changes are consistent with the expected widespread consequences of marine warming (Montes Huugo et al. 2009). A reduction in diatoms in the diet of Antarctic krill is likely to reduce both growth and reproduction (Ross et al. 2000, Schmidt et al. 2012). Thus, the most likely effects of plausible changes in chlorophyll-a concentration are in the range between our reduced and unchanged chlorophyll scenarios.

CMIP5-class models are being increasingly used to investigate climate impacts on marine species (Stock et al. 2011). These models have many uncertainties, including regional biases and differences between models. Our results confirm a regional bias in Southern Ocean SST (Sallée et al in press). The representation of some Southern Ocean features, such as the ACC, has improved in CMIP5 compared to the previous generation of model results (Meijers et al. 2012). Nonetheless, the available models generally have low skill in reproducing sea ice, which is a critical influence on SST (Turner et al 2013; Sallée et al in press). The models differ markedly from each other in terms of both the magnitude and spatial distribution of SST. We have followed recommended practice for controlling and assessing the influence of these model uncertainties on our results (Stock et al 2011). It is clear from Fig. 4 that most models are in agreement that the ACC will experience significant warming.

The degradation of Antarctic krill growth habitat in the ACC is likely to have severe consequences for predators at South Georgia. Analysis of foodweb models suggests that predators able to take advantage of copepod production might be relatively unaffected by a severe reduction in Antarctic krill availability, but that the majority of air-breathing predator populations at South Georgia are likely to experience significant declines (Hill et al. 2012).

Our results also have implications for the management of the Antarctic krill fishery, which took 68% of its total catch between 1980 and 2011 from the area of projected severe habitat degradation (Hill

2013). Management must acknowledge the twin realities of climate-driven ecosystem change and growing demand for fishery resources. A recommendation that the Commission for the Conservation of Antarctic Marine Living Resources, which is responsible for managing the Antarctic krill fishery, should increase consideration of climate change impacts in its management decisions was made in 1992 (Everson et al 1992) but it was not until 2009 that the Commission resolved to do so (http://www.ccamlr.org/en/resolution-30/xxviii-2009). The imminent risks posed by climate change suggest a need for more rapid progress.

CONCLUSIONS

Most available projections imply significant warming of the ACC by the late 21st century. This warming is likely to severely diminish the biomass production of Antarctic krill. The most severe impacts are likely to occur within the foraging ranges of the seabirds and seals which breed at South Georgia, and which represent substantial fractions of the global populations of these species. This is also the main area where the Antarctic krill fishery operates. Our results provide strong and specific evidence that climate change poses a threat to Antarctic krill growth habitat and consequently to Southern Ocean biodiversity and ecosystem services. There is a need to develop methods for evaluating these impacts in parallel with improved regional climate projections. CCAMLR and the authorities responsible for managing other human activities in the Southern Ocean should prioritise adaptation to and management of the risks posed by climate change.

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Table 1. The climate models used in this study.

Model name	Modelling group	Number of realisations			Global number of SST grid points		SST on regular grid?
		RCP2.6	RCP4.5	RCP8.5	Longitudinal	Latitudinal	
BCC-CSM1.1	Beijing Climate Center, China Meteorological Administration	1	1	1	360	232	No
CanESM2	Canadian Centre for Climate Modelling and Analysis	5	5	5	256	192	Yes
CNRM-CM5	Centre National de Recherches Météorologiques / Centre Européen de Recherche et Formation Avancée en Calcul Scientifique	1	1	5	362	292	No
CSIRO-Mk3.6.0	Commonwealth Scientific and Industrial Research Organization in collaboration with Queensland Climate Change Centre of Excellence	10	10	10	192	189	Yes
EC-EARTH	EC-EARTH consortium	2	9	9	362	292	No
GFDL-ESM2G	NOAA Geophysical Fluid Dynamics Laboratory	1		1	360	210	No
GISS-E2-R	NASA Goddard Institute for Space Studies	1	5	1	144	90	Yes
HadGEM2-CC	Met Office Hadley Centre (additional HadGEM2-ES realizations contributed by Instituto Nacional de Pesquisas Espaciais)		1	3	360	216	Yes
HadGEM2-ES		4	3	4	360	216	Yes
INM-CM4	Institute for Numerical Mathematics		1	1	360	340	No
IPSL-CM5A-LR	Institut Pierre-Simon Laplace	3	4	4	182	149	No
IPSL-CM5A-MR		1	1	1	182	149	No
MIROC5	Atmosphere and Ocean Research Institute (The University of Tokyo), National Institute for Environmental Studies, and Japan Agency for Marine-Earth Science and Technology	3	3	3	256	224	No
MPI-ESM-LR	Max-Planck-Institut für Meteorologie (Max Planck Institute for Meteorology)	3	3	3	256	220	No
MRI-CGCM3	Meteorological Research Institute	1	1	1	360	368	No
NorESM1-M	Norwegian Climate Centre	1	1	1	320	384	No

The table lists the models used in this study, identifies the number of realisations (individual model runs) available for each of the three Representative Control Pathways (RCPs 2.6, 4.5 and 8.5), and specifies the spatial resolution and grid type for each model. Within each RCP, the sea surface temperature (SST) estimates for each model were calculated as the mean of the estimates for all realisations available for that model.
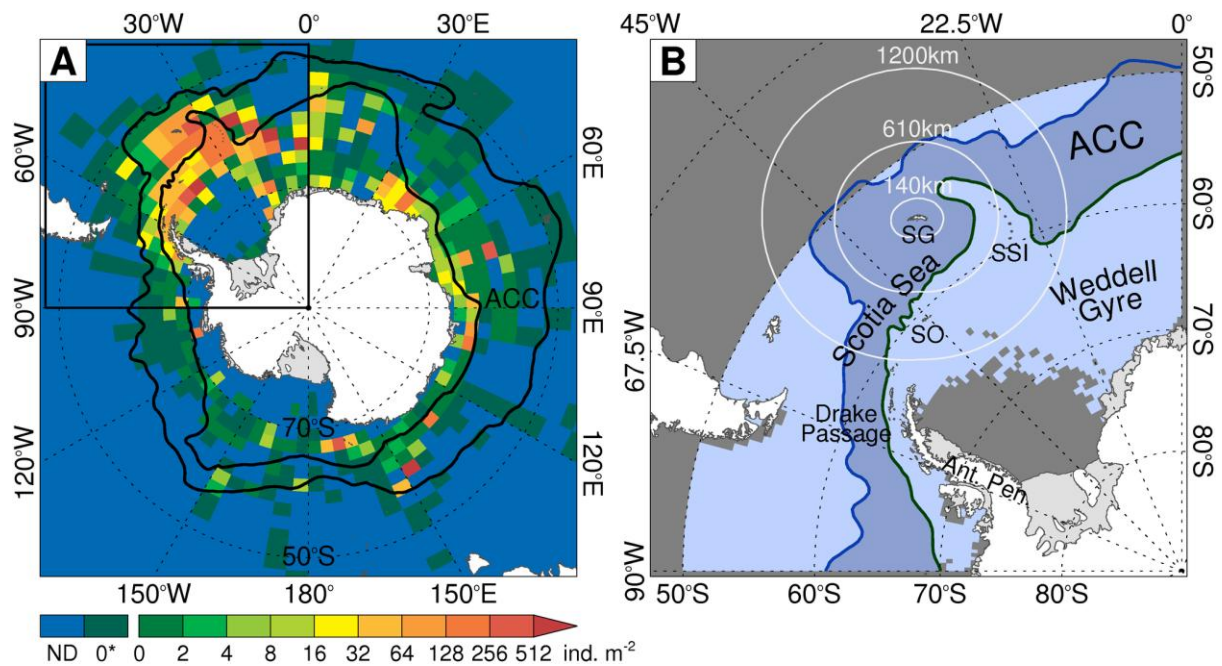
Figure 1. The distribution of Antarctic krill and the study area.

(A) The observed distribution of Antarctic krill (individuals m^{-2} within each 5° longitude by 2° latitude grid cell, ND = no data, 0*= no krill recorded in the available data) from [12]. (Inset & B) The study area, showing the Antarctic Circumpolar Current (ACC) which is bounded to the north by the Antarctic Polar Front and to the south by the Southern boundary of the ACC) (southern circumpolar black line) (Positions from [34]). The concentric distances from South Georgia (SG) indicate the approximate foraging ranges of representative predators of Antarctic krill: Antarctic fur seals (140 km), Wandering albatrosses (610 km) and Grey-headed albatrosses (1200 km). Areas north of 50°S (shaded grey) were not included in the study. Ant. Pen = Antarctic Peninsula, SO=South Orkney Islands, SSI= South Sandwich Islands.
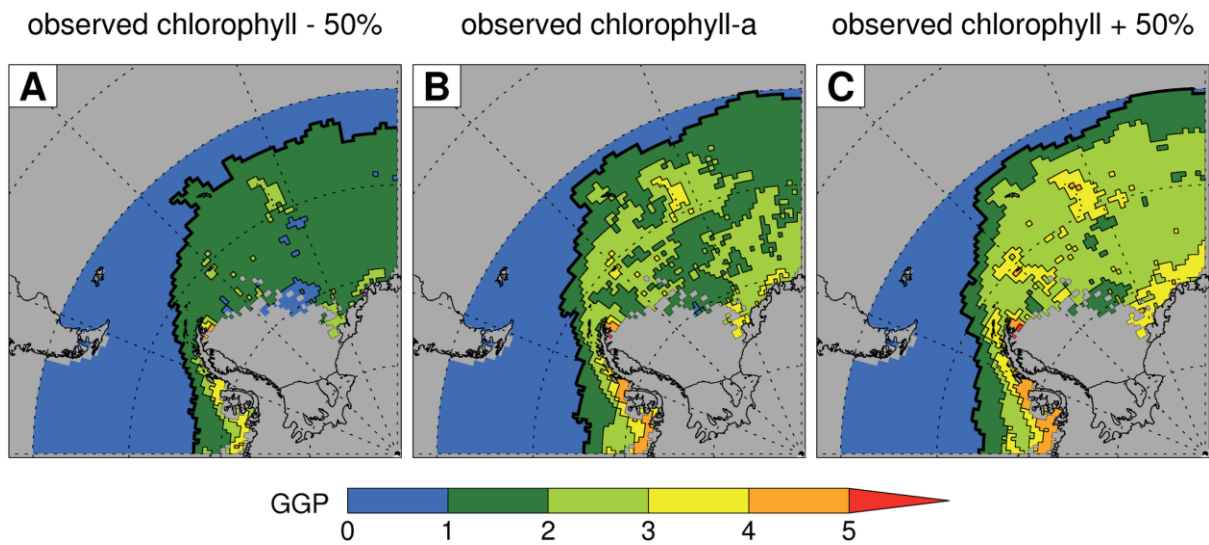
Figure 2. Current Antarctic krill summer growth habitat quality and sensitivity to chlorophyll concentration.

 (A) Gross Growth Potential (GGP, a unitless quantity which indicates the potential proportional increase in the mass of an individual Antarctic krill during a single summer and is therefore a measure of habitat quality) calculated for a 40 mm individual using observed SSTs (for the period 2002 to 2011), and observed chlorophyll-a concentrations (for the period 1997-2010) reduced by 50%. (B) Estimated current GGP calculated using observed SSTs, and observed chlorophyll-a concentrations. (C) GGP calculated using observed SSTs, and observed chlorophyll-a concentrations increased by 50%. The spatial resolution is 1° longitude by 0.5° latitude and the thick black line indicates the northern extent of the current growth area (the habitat that supports Antarctic krill growth).
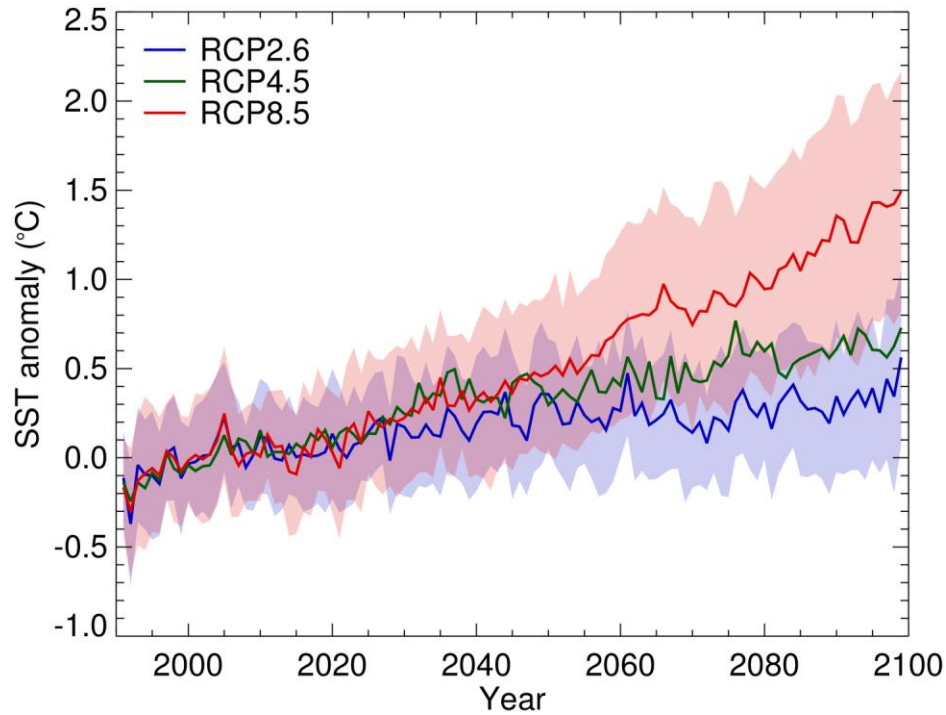
Figure 3. Projected 21ˢᵗ Century summer surface warming of the Southern Ocean between 0° and 90°W.

Projected summer (January to March) sea surface temperature (SST) anomaly for the region between 0° and 90°W and south of the Antarctic Polar Front (Fig. 1). The SST anomaly is the within-year mean of spatially resolved summer SSTs for a specific model realisation minus the 1991-2020 mean of spatially resolved summer SST for the same model realisation. The coloured lines indicate the mean SST anomaly for 1991-2099 across all relevant models (Table 1) for each of three Representative Control Pathways (RCPs 2.6, 4.5 and 8.5) and the shaded envelopes indicate the between-realisation standard deviation for RCPs 2.6 and 8.5.
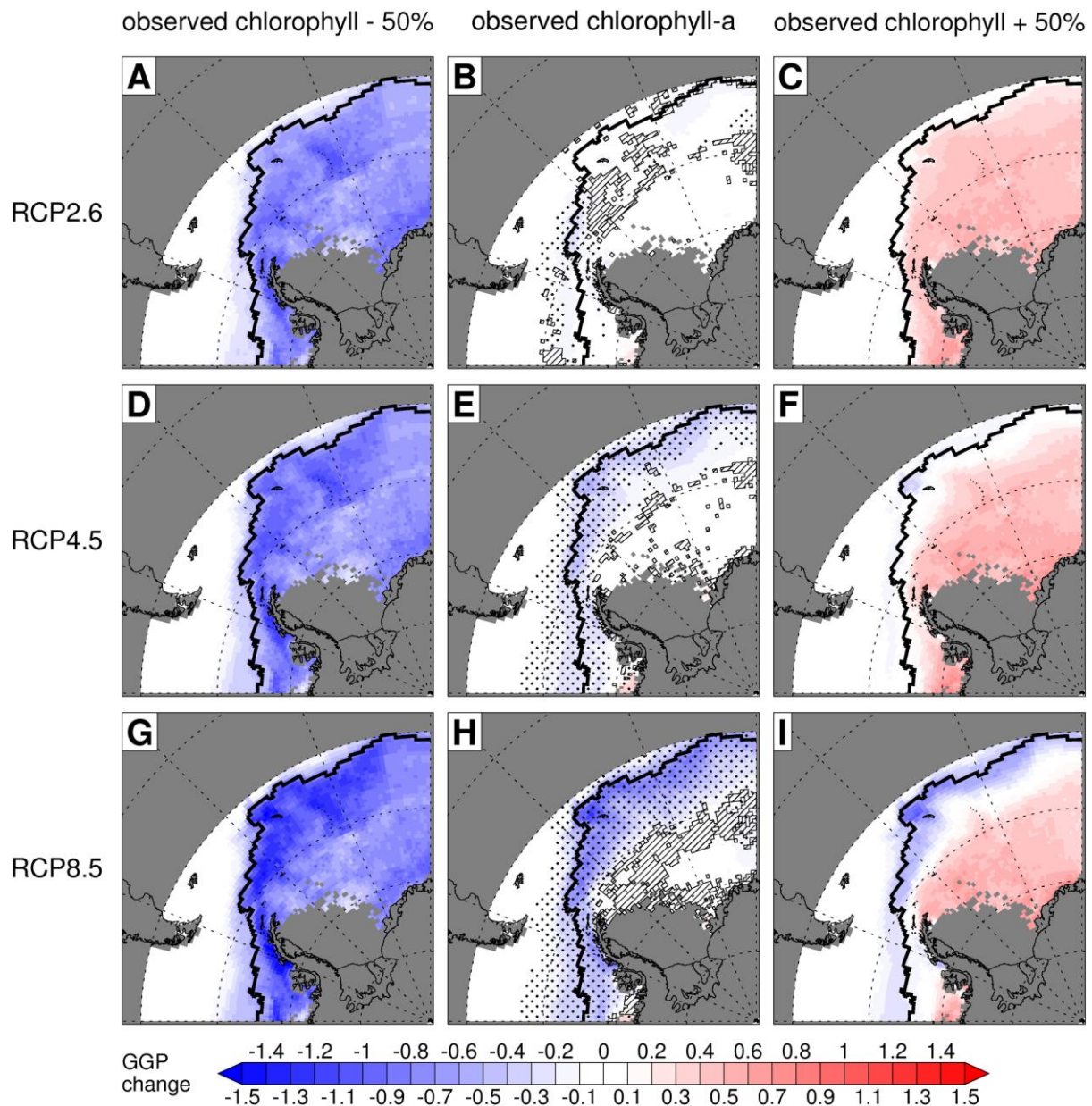
**Figure 4. Spatial pattern of projected change in Antarctic krill habitat by the late 21st Century.**

Each panel shows the projected GGP change (GGP for the period 2070-2099 minus estimated current GGP, as shown in Fig. 2B) calculated across multiple climate models. The GGP values were calculated using bias-corrected SSTs from either RCP2.6 (A, B & C); RCP4.5 (D, E & F) or RCP8.5 (G, H & I) and either observed chlorophyll-a concentrations reduced by 50% (A, D & G); observed chlorophyll-a concentrations (B, E & H); or observed chlorophyll-a concentrations increased by 50% (C, F & I). Additional symbols (B, E & H) indicate the degree of concordance between climate models. Cells where fewer than 50% of the models project significant change (t-test P ≤ 0.05) from the current period have no additional symbol; cells where 50% or more of the models project significant change are highlighted with stippling if 90% or more of models agree on the sign of the change and are highlighted with hatched lines if fewer than 90% agree. The spatial resolution is 1° longitude by 0.5° latitude and the thick black line indicates the northern extent of the current growth area (Fig. 2B).
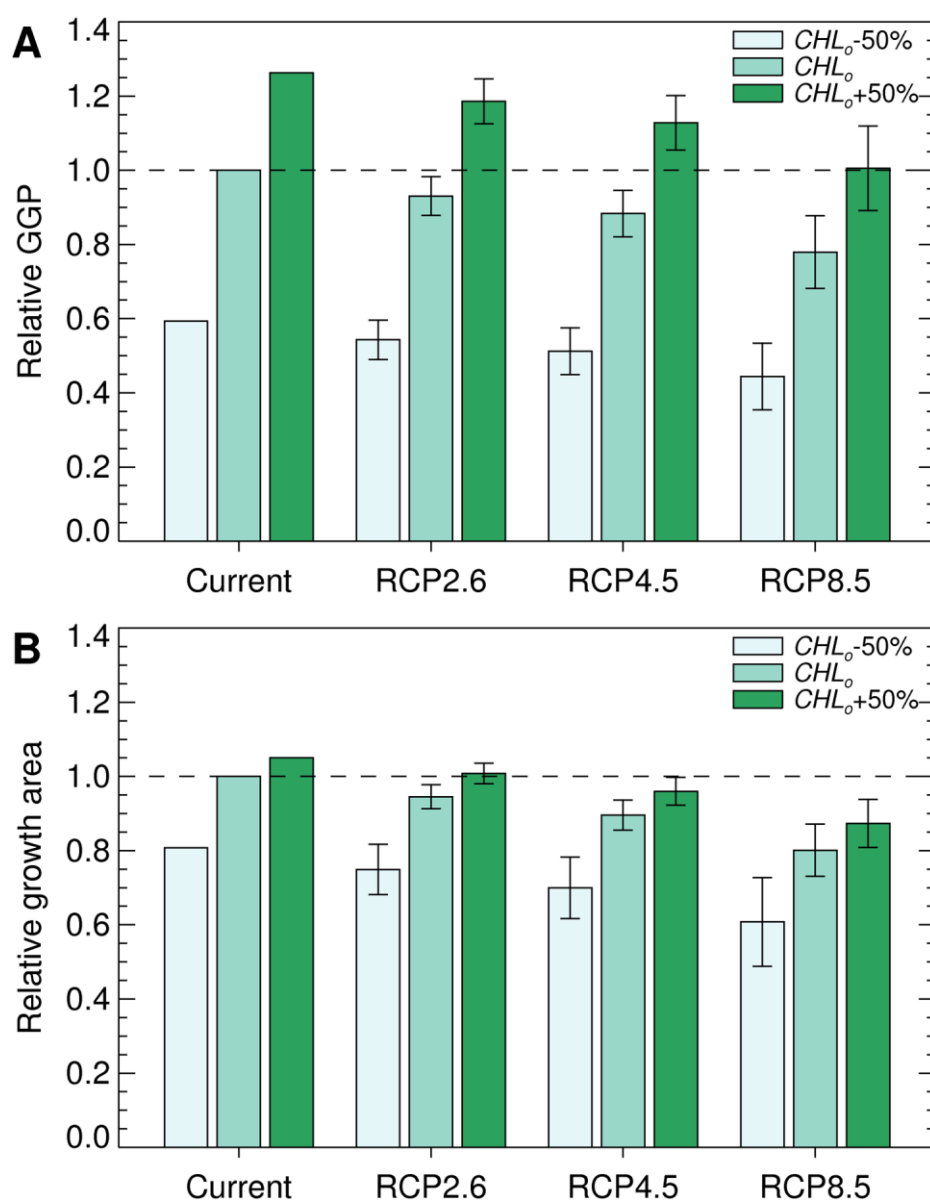
Figure 5. Projected change in Antarctic krill habitat in the study area by the late 21st Century.

Relative GGP (GGP for the period 2070-2099 divided by estimated current GGP) (A) and relative growth area (growth area for the period 2070-2099 divided by estimated current growth area) (B), calculated for the study area (Fig. 1B). Results were calculated across multiple models using bias-corrected SSTs from either RCP2.6, RCP4.5 or RCP8.5, and either observed chlorophyll-a concentrations reduced by 50% (CHL_o-50%), observed chlorophyll-a concentrations (CHL_o) or observed chlorophyll-a concentrations increased by 50% (CHL_o+50%). The error bars show the between-model standard deviation.
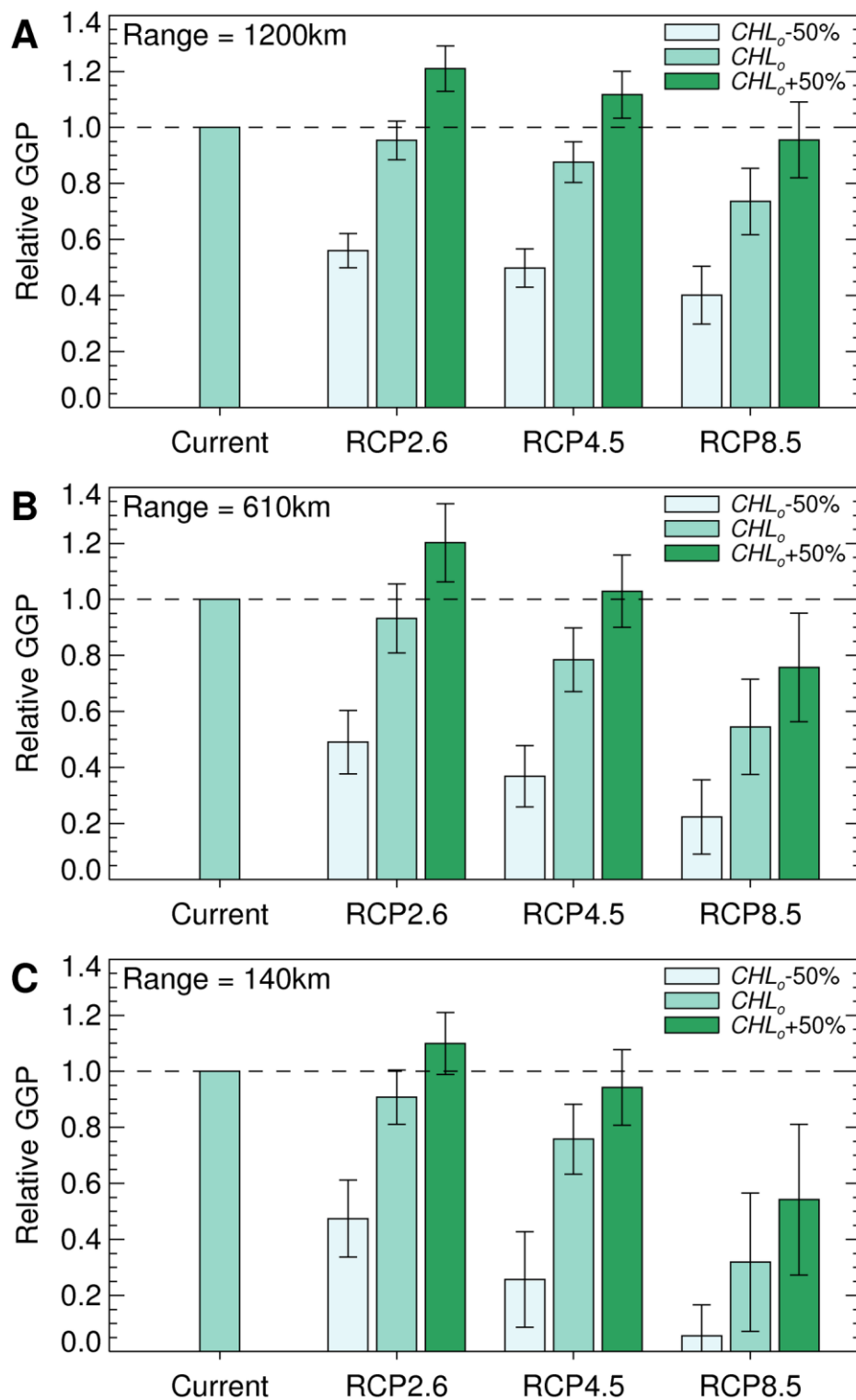
Figure 6. Projected change in Antarctic krill habitat accessible to predators at South Georgia.

Relative GGP (GGP for the period 2070-2099 divided by estimated current GGP), calculated within the area accessible to predators with foraging ranges of 1200 km (A), 610 km (B) and 140 km (C) from South Georgia. Results were calculated across multiple models using projected SSTs from either RCP2.6, RCP4.5 or RCP8.5, and either observed chlorophyll-a concentrations reduced by 50% (CHL_o+50%), observed chlorophyll-a concentrations (CHL_o) or observed chlorophyll-a concentrations increased by 50% (CHL_o-50%). The error bars show the between-model standard deviation.