

Evaluating Antarctic marine protected area scenarios using a dynamic food web model



Adrian Dahood^{a,b,c,†}, Kim de Mutsert^{a,*}, George M. Watters^b

^a Department of Environmental Science and Policy, George Mason University, 4400 University Drive, Fairfax, VA 22030, USA

^b Antarctic Ecosystem Research Division, Southwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 8901 La Jolla Shores Drive, La Jolla, CA 92037-1023, USA

^c University of California Santa Cruz, Institute of Marine Sciences, Mailstop: Ocean Science 1156 High Street, Santa Cruz, CA 95064, USA

ARTICLE INFO

Keywords:
 Dynamic trophic model
 Ecospace
 Krill
 Antarctic Peninsula
 Marine protected area
 No-take reserves

ABSTRACT

Marine protected areas, especially when they are or include no-take zones, can support conservation objectives by creating an area where marine organisms are protected from human disturbances, particularly fishing. The coast of the Antarctic continent is the only habitat of the iconic Adélie penguin, whose main diet is Antarctic krill. Current threats to Adélie Penguins, other Antarctic krill predators and Antarctic krill itself include sea-ice loss as a result of climate change and krill fishing. We use a spatially and temporally dynamic food web model of the region surrounding the Western Antarctic Peninsula to evaluate the potential impacts of various marine protected area scenarios in the context of climate change. We examine the effects of sustained sea-ice loss on krill and seven monitored krill predators. We evaluate four marine protected area scenarios given two scenarios that describe future changes in sea ice and three scenarios that describe future changes in krill fishing effort. Our results indicate that establishing no-take zones where krill might aggregate in the future and where some krill predators forage could positively affect biomass accumulation of krill and the predators. No-take zones may be particularly important for enhancing the resilience of species that have recently experienced population decline and ensuring positive outcomes from establishing a marine protected area in the region. Our simulations suggest that establishing protected areas in the right locations can play an important role in mitigating the negative effects of climate change on iconic species that many people want to conserve.

1. Introduction

Climate change is affecting marine biomes and the communities, species, and habitats within them (Scheffers et al., 2016). The western Antarctic Peninsula is a region where climate change is causing rapid change to the ecosystem, resulting in the loss of sea-ice habitats (Stammerjohn et al., 2008) on which many species in the region are dependent. Antarctic krill (*Euphausia superba*; hereafter krill), an important forage species to marine birds, mammals, and fishes, are experiencing increased fishing pressure, resulting in increased risks to krill predators (Klein et al., 2018; Watters et al., 2020). Protecting areas from fishing impacts, by establishing no-take zones, can be a useful management tool in the conservation of marine ecosystems that are exposed to multiple threats (Roberts et al., 2017).

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR, hereafter referred to as “the Commission”) is

responsible for managing marine living resources south of the Antarctic Convergence using an ecosystem-based approach to management (Constable et al., 2000), e.g., by explicitly considering the needs of krill predators within its management strategy for the krill fishery. The Commission's overarching management objective is to conserve Antarctic marine living resources. The Commission has heard global calls to protect significant portions of the World Ocean (e.g., from the 2002 United Nations World Summit on Sustainable Development) and recognized that its conservation objective could be met by creating marine protected areas (SC-CAMLR, 2005, paragraphs 3.54 i, iii, iv-b and iv-c). In 2008, the Commission prioritized establishing a system of marine protected areas that encompasses a representative assortment of marine biomes, communities, species and habitats within the Antarctic (CCAMLR, 2008, paragraphs 7.3 and 7.4). In 2011, the Commission adopted the “General Framework for the Establishment of CCAMLR Marine Protected Areas” (CM 91-04; CCAMLR, 2011 paragraph 2;

* Corresponding author.

E-mail address: kdemutse@gmu.edu (K. de Mutsert).

† Deceased 2 September 2019.

hereafter referred to as “the framework”) which sets out a set of objectives particular to marine protected areas. Included in this list of objectives are representative protection of biodiversity, preservation of ecosystem processes and functions, maintenance of resilience or the ability to adapt to climate change, and distinguishing the effects of climate change from those of fishing.

Work is underway to develop a new marine protected area around the Western Antarctic Peninsula and Southern Scotia Arc (CCAMLR, 2017, 122 pp. available at: https://www.ccamlr.org/en/system/files/e-cc-xxxvi_0.pdf; paragraphs 5.63–5.69). This region is known as “Planning Domain 1” and is characterized by marine food webs in which krill play a central role (Ballerini et al., 2014; Constable et al., 2000). The krill fishery is the largest Antarctic fishery (by tonnage; Nicol et al., 2012) and fishers remove up to 155,000 t of krill annually from the waters offshore of the Western Antarctic Peninsula (CCAMLR, 2018). The relative amounts of krill consumed by its various predators have likely changed as the abundances of krill-eating penguins (Lynch et al., 2012), fishes (Kock and Jones, 2005) and especially whales (Zerbini et al., 2019) have themselves changed. The Western Antarctic Peninsula is also experiencing sustained warming and significant sea-ice loss (Ducklow et al., 2013). There is already evidence of changes in the patterns of distribution and abundance of krill (Atkinson et al., 2019; Atkinson et al., 2004) and krill predators (Lynch et al., 2012) associated with warming. It seems likely that warming will continue in the region (IPCC, 2013), and that the marine ecosystem will continue to change. Specifically, species' distributions and abundances and the locations of certain ecosystem processes and functions may continue to change in response to sustained changes in the abundances of animals like whales, warming, and sea-ice loss.

Marine protected area planning processes undertaken by the Commission have relied heavily on models and analyses that use static maps describing human use and biodiversity patterns (see Brooks, 2013 for a summary). One assumption that often underlies the use of static maps is that the spatial distribution of biodiversity and human use will not change significantly in the foreseeable future. In rapidly changing regions like the Western Antarctic Peninsula, it seems beneficial to move beyond the assumption of a static environment and leverage dynamic modeling that explicitly considers changing environmental conditions in the planning process. Thus, to facilitate the development of a marine protected area in the Western Antarctic Peninsula and identify features that seem likely to lead to a more effective marine protected area for the region, we use such an approach to explicitly consider changing sea ice to evaluate marine protected area scenarios.

The Ecospace module of the software package Ecopath with Ecosim allows for spatially and temporally dynamic simulations to evaluate the impacts of environmental drivers on fisheries management strategies, including marine protected areas (Christensen and Walters, 2004) using an ecosystem-based approach. We previously developed a mass-balanced (Ecopath) model that was successfully calibrated and recreated trends in the abundances (in Ecosim) of key monitored species in the Western Antarctic Peninsula (Dahood et al., 2019). The objective of this study, by advancing that model into a spatial setting (via Ecospace), is to evaluate marine protected area scenarios in the context of changing sea-ice conditions. We use this Ecospace model to evaluate four marine protected area scenarios and identify features that may improve the efficacy of a marine protected area around the Western Antarctic Peninsula. By including varying levels of sea-ice loss and future fishing pressure in a scenario analysis, we can simultaneously distinguish the effects of climate change from those of fishing and demonstrate the efficacy of establishing no-take zones to achieve desirable conservation outcomes in a rapidly changing environment.

2. Methods

2.1. Underlying model

The study area was FAO Statistical Subarea 48.1, which includes the Western Antarctic Peninsula (CCAMLR, 2018). A mass balanced food web model (Ecopath) and calibrated, time-dynamic simulations (Ecosim) for the years 1996–2012 (described by Dahood et al., 2019) underpin the spatial model. This study thereby uses a published model for which model performance, calibration, and confidence has been described in Dahood et al. (2019). The food web is represented by 35 groups that range from plankton to apex predators. The model was calibrated to time-series data describing trends in krill biomass and trends in the abundances of seven krill predators: Adélie penguin (*Pygoscelis adeliae*), chinstrap penguin (*P. antarcticum*), gentoo penguin (*P. papua*), Antarctic fur seal (*Arctocephalus gazella*), mackerel icefish (*Champscephalus gunnari*), marbled rockcod (*Notothenia rossii*), and humped rockcod (*Gobionotothen gibberifrons*). The model recreated trends for all eight species at monthly time steps when temporally dynamic measures of the sea-ice regime were included as forcing functions (Dahood et al., 2019).

The study area is simplified and represented as a grid within Ecospace. Our Ecospace model has a grid cell resolution of 100 km² and contains approximately 6100 active cells where depth was greater than 0 m. Ecospace simulations include Ecosim simulations within each grid cell but add spatial data describing environmental conditions and foraging areas (Christensen and Walters, 2004). Spatial layers input into Ecospace include bathymetry (Carbotte et al., 2007), average primary production during the austral summer for the years 1997–2012 (Acker and Leptoukh, 2007; SeaWifs data 1997–2010 and MODIS data 2010–2012 accessed through the Giovanni online data system), monthly sea-ice concentration for the years 1996–2012 (Cavalieri et al., 1996, updated yearly), locations of fishing effort at the scale of “small scale management units” designated by CCAMLR (data provided in CCAMLR, 2018) and “habitat capacity” maps describing the potential foraging area of each model group (Christensen et al., 2014 see Appendix A).

The Ecospace model uses monthly time steps and biomass can move across grid cells at every time step. Movement rates were calculated from published swim speeds (Appendix B). Movement in Ecospace is based on a random walk (Christensen and Walters, 2004). The random walk does not allow directional movement to be modeled, but the software allows users to direct species' relative dispersals towards more suitable habitats (Christensen et al., 2014).

The Ecospace model was tuned to data collected during 1996–2012. The model was considered tuned when it was able to recreate general trends in species' distribution and abundance, as documented in the literature. For example, during the period 1996–2012, krill biomass declined and the relative importance of habitats in southern areas around the Western Antarctic Peninsula increased (Atkinson et al., 2004; Atkinson et al., 2009). The model was considered tuned for krill when it recreated this broad spatial pattern. Tuning was accomplished by using spatially and temporally dynamic monthly maps of sea-ice concentration (Cavalieri et al., 1996, updated yearly) to influence the spatial distributions of modeled groups. Functional response curves were used to describe how species respond to sea-ice conditions and were applied to krill and twelve other model groups to tune the model (see Appendix C for details).

2.2. Scenarios

To evaluate marine protected area efficacy in varying conditions we

created several 100-year scenarios, all of which included the same 17-year tuning period (1996–2012). Sea-ice conditions, fishing pressure, and marine protected area placement varied among scenarios. While whales (killer whales, sperm whales, blue whales, fin whales, minke whales, and humpback whales) are included in the model, and their consumption of krill is represented dynamically in our scenarios, we did not vary whale predation among scenarios, since our focus was on evaluating the establishment of marine protected areas.

We evaluated two sea-ice scenarios. Both sea-ice scenarios employ monthly maps of sea-ice concentration for the years 1996–2012 (Cavalieri et al., 1996, updated yearly) and use these maps in the same sequence for the first 17 years of the simulation (1996–2012). We randomly selected years, and their corresponding maps, to build the remaining years of the time series. The first sea-ice scenario represents conditions continuing as they were from 1996 to 2012 (the “status quo ice” scenario). In this scenario, the ice maps from every year during 1996–2012, had an equal probability of being selected and being inserted into the simulation. The second sea-ice scenario represents decreasing sea ice and favors years with less sea ice as time progresses (the “decreasing ice” scenario). To build this scenario, we used a biased selection function to preferentially choose those years within 1996–2012 with less sea ice, and their corresponding maps, for the remaining 83 years of the simulation. The monthly maps of sea-ice concentration were introduced to the model as ASCII text files using an external data framework (Steenbeek et al., 2013). All other environmental conditions were matched to the selected year in the sea-ice scenario (see Appendix D for details).

We evaluated three scenarios that describe fishing in the future. The *status quo* fishing scenario is based on average monthly fishing effort calculated from data describing fishing during 2009–2012 (CCAMLR, 2018). This scenario represents the effort expended to catch approximately 125,000 t of krill per year. To create the remaining two fishing scenarios, we multiplied the monthly averages from the *status quo* scenario by approximately five (5× fishing) and twelve (12× fishing). The 5× fishing scenario thus represents the effort needed to catch approximately 620,000 t within Statistical Subarea 48.1. The 12× fishing scenario represents the amount of fishing effort needed to catch over 1.4 million tonnes in this subarea, which is 25% of the full precautionary catch limit for krill (CCAMLR, 2016).

Fishing also has a spatio-temporal component which is incorporated in the model at monthly intervals as a dynamic “cost” layer. The Commission summarizes krill-fishery data at the scale of small scale management units (referred to as units hereafter), eight of which are located within Statistical Subarea 48.1 (CCAMLR, 2018). For the years 1996–2012, the “cost” was set prohibitively high for all grid cells contained in units that were not fished during a particular time step. Fishing was therefore restricted to the units in which it was reported to occur each month. For the remainder of the simulation, at each monthly time step, fishing was allowed to occur in every cell that had less than 50% sea-ice concentration during a time step (Jones and Parker, 2016). The cost of fishing was set prohibitively high in grid cells with ≥50% sea-ice concentration.

We evaluated four marine protected area scenarios (Fig. 1). Ecospace treats all marine protected areas as no-take marine reserves (Christensen and Walters, 2004). The first two marine protected area scenarios were derived from the preliminary proposal submitted to the Commission by the Delegations of Argentina and Chile (Delegations of Argentina and Chile, 2017b). The first marine protected area scenario included all portions of the proposed “General Protection Zone” that occur within Statistical Subarea 48.1 (hereafter D1MPA). The second marine protected area scenario only included the more northern regions of the D1MPA scenario (hereafter D1MPAN). The third and fourth marine protected area scenarios were derived from priorities articulated at a U.S. stakeholder workshop held in La Jolla, California (Watters, 2015). In the third marine protected area scenario, the top 10% of areas prioritized for protection by U.S. stakeholders and within

Subarea 48.1 were protected (hereafter US10). In the fourth marine protected area scenario, only the southern portion of the US10 scenario (hereafter US10S) was protected. We note that only the D1MPA scenario has been put forward to the Commission for consideration as a candidate marine protected area, and the three other scenarios considered here serve largely to learn more about the D1MPA.

3. Results

Our results indicate fishing scenarios and marine protected area scenarios had larger impacts on model outcomes than sea-ice scenarios; the magnitudes and general trends of biomass accumulation were similar across sea-ice scenarios (Appendix E). It is possible the sea-ice scenarios considered here were too similar to yield dramatic differences in model outcomes. The sampling procedure to create the decreasing ice scenario may not have been sufficiently extreme, or the ice maps from 1996 to 2012 may not adequately capture how future sea-ice loss will manifest in the region. Because the results from our two sea-ice scenarios were so similar, we only show results from the decreasing ice scenario in the remainder of this paper as sustained ice loss seems likely for the region (IPCC, 2013).

Fishing scenario (Status Quo, 5×, or 12×) influenced biomass outcomes and the efficacy (or lack thereof) of no-take reserves. As fishing pressure increased, the modeled biomasses of krill and krill-dependent predators decreased and, relative to a scenario without a marine protected area, the effectiveness of no-take reserves increased (Fig. 2). The best performing marine protected areas slowed modeled declines for some species.

Ecospace uses a gravity model to draw fishing effort into cells that have high concentrations of the target species (in this case krill) and low “cost”. In this study, after the model calibration period, cost was defined by sea-ice concentration. When a marine protected area scenario did not encompass areas of krill concentration within a no-take reserve, the modeled distribution of fishing effort resembled that of krill; fishing effort concentrated in the same locations as krill biomass (Fig. 3). When a marine protected area was not simulated, the distribution of fishing effort was practically indistinguishable from that of krill at the end of the calibration period (compare Fig. 1 to the far-left panel in Fig. 3). Focused fishing in the southern part of the study area where krill concentrated was sufficient to disrupt this concentration; the southern area of krill concentration persisted only when it was included within the boundaries of a no-take reserve (Fig. 4).

When krill concentrated in a marine protected area, the total biomass of krill in the system increased relative to simulations in which there was no marine protected area or an ineffective marine protected area. The D1MPA, US10, and US10S scenarios all resulted in an increase in krill in the system (Fig. 5). These same three scenarios also resulted in modest increases in the biomasses of Adélie penguins and Antarctic fur seals (Fig. 5). This is notable because all three species experienced declines in biomass or abundance during the model calibration period (Krill: Atkinson et al., 2004; Antarctic fur seals: Goebel and Reiss, 2014; Adélie penguins: Lynch et al., 2012). The US10S scenario, which protected only the southern area of krill concentration, was the most effective at protecting krill and Adélie penguins. The D1MPA and D1MPAN scenarios benefitted chinstrap and gentoo penguins (Fig. 5). These two marine protected area scenarios protected the foraging grounds of chinstrap penguins near Elephant Island and of gentoo penguins inside the Bransfield Strait (Delegations of Argentina and Chile, 2017b); these areas were not protected by the US10 and US10S scenarios. While gentoo penguins are currently increasing, chinstrap penguins are currently declining (Lynch et al., 2012). The results for the three fish species indicated that none of the marine protected area scenarios considered here had sustained impacts on their biomasses (Fig. 5).

The marine protected area scenarios impacted the spatial distribution of fishing (e.g., Fig. 3) and the total catch. Because the marine

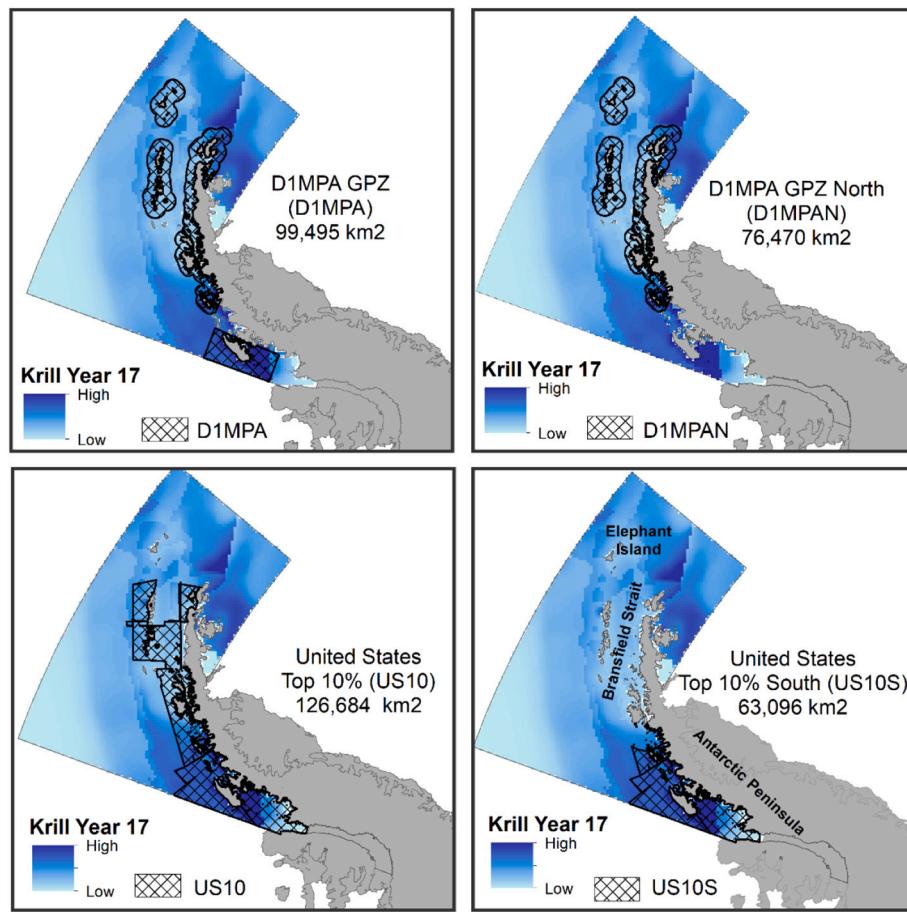


Fig. 1. Areas and placements marine protected area scenarios evaluated here. The underlying colored layer illustrates the spatial distribution of krill in 2012 at the end of the model calibration period. Darker blue indicates more krill biomass. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

protected areas were modeled as no-take reserves, fishing effort was displaced and directed towards any available krill concentration outside the boundaries of the marine protected area. For the D1MPA and D1MPAN scenarios, this manifested as a concentration of fishing effort in more northern and offshore waters. For the US10 and US10S scenarios, this manifested as a concentration of effort along the marine protected area boundaries. Under 5 × fishing pressure, all four marine protected area scenarios decreased total catch relative to a scenario in which no marine protected area was simulated (Fig. 6). However, the model indicated the D1MPA scenario would have the smallest impact, reducing catch by only 1.25%.

4. Discussion

Our results suggest that a well-placed, no-take reserve could, relative to the case without such a reserve, increase the biomass of krill (the target species) and some krill predators (iconic species that many people want to conserve). In the area of investigation, the Western Antarctic Peninsula, the benefitting species indeed not only included the target species Antarctic krill, but also some of its predators such as Adélie penguins, Antarctic fur seals, chinstrap penguins and gentoo penguins. All these species are affected by climate change (Constable et al., 2014); establishing a protected area has the potential to increase the resilience of these species to a rapidly changing environment with declining food sources.

The model presented here builds on a previously calibrated food web model built in Ecopath and time-dynamic simulations of that food web in Ecosim (Dahood et al., 2019) by adding tuned, spatially and temporally dynamic simulations in Ecospace. This is a significant advancement over other available Ecopath with Ecosim models for the region, as no published models describing this system were developed

into spatial models (Ballerini et al., 2014; Cornejo-Donoso and Antezana, 2008; Suprenand and Ainsworth, 2017). Only one model in the grey literature included Ecospace simulations and these were not tuned or based on calibrated, time-dynamic simulations in Ecosim (Erfran and Pitcher, 2005). Both the calibration (Dahood et al., 2019) and tuning process presented here were accomplished by using sea-ice dynamics to force the model.

The food web in the study area is often described as krill-centric and many predators include krill as a significant part of their diet. Thus, we attempted to ensure that the model performed adequately for krill. Despite the model's inability to explicitly include directional movement patterns of krill (Reiss et al., 2017; Richerson et al., 2015), it was able to successfully capture a southward contraction of krill that seems to have occurred during the tuning period (Atkinson et al., 2019), and our results are consistent with other modeling efforts indicating that more southern coastal areas in the Antarctic Peninsula region may increase in importance as krill habitat with continued warming (Hill et al., 2013). We therefore assert that our model is suitable for exploring marine protected area scenarios in the region. We note, however, that our model is not presently capable of exploring hypotheses that relate to whether Antarctic silverfish (*Pleuragramma antarcticum*) will replace krill as a primary forage species in the Antarctic Peninsula region. Antarctic silverfish are not represented in our model (Dahood et al., 2019), but, historically, this species was an important prey of penguins (Emslie and Patterson, 2007) and can provide energy-rich food that promotes the survival of penguin chicks (Chapman et al., 2011).

In our simulations, the two species that benefitted most from a no-take reserve were krill and Adélie penguins. The D1MPA, US10 and US10S scenarios provided the greatest benefits. These three marine protected area scenarios all offer protection in the southern area where the model indicates that krill may concentrate. When the simulated

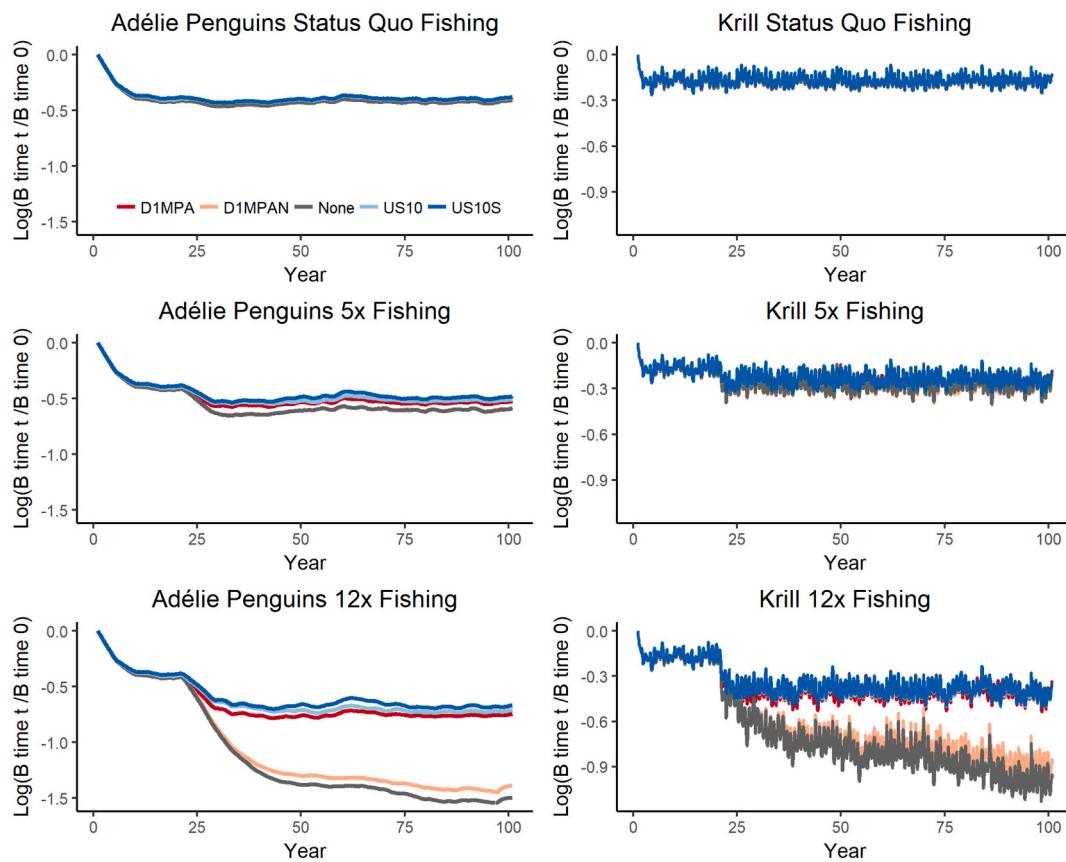


Fig. 2. Model results for Adélie penguins and large krill under varying fishing pressure. Line color denotes marine protected area scenario with trajectories from a scenario without a marine protected area in grey. The y-axis denotes the logarithm of the ratio between the biomass (B) at time t divided the biomass at time zero. Negative values indicate a biomass decline relative to the start of the simulations. The first 17 years of each simulation represent the model calibration period.

fishery did not remove krill from the southern krill concentration, more krill biomass was present in the system and Adélie penguins that nest in the southern part of the study area (Lynch et al., 2012; Second WS-MPA Domain 1, 2015) benefitted. Antarctic fur seals, chinstrap penguins and

gentoo penguins also benefitted from no-take reserves. However, for these species, the D1MPA scenario was most effective. Chinstrap penguins (Lynch et al., 2012) and Antarctic fur seals (Goebel and Reiss, 2014) are currently experiencing declines, and an effective marine

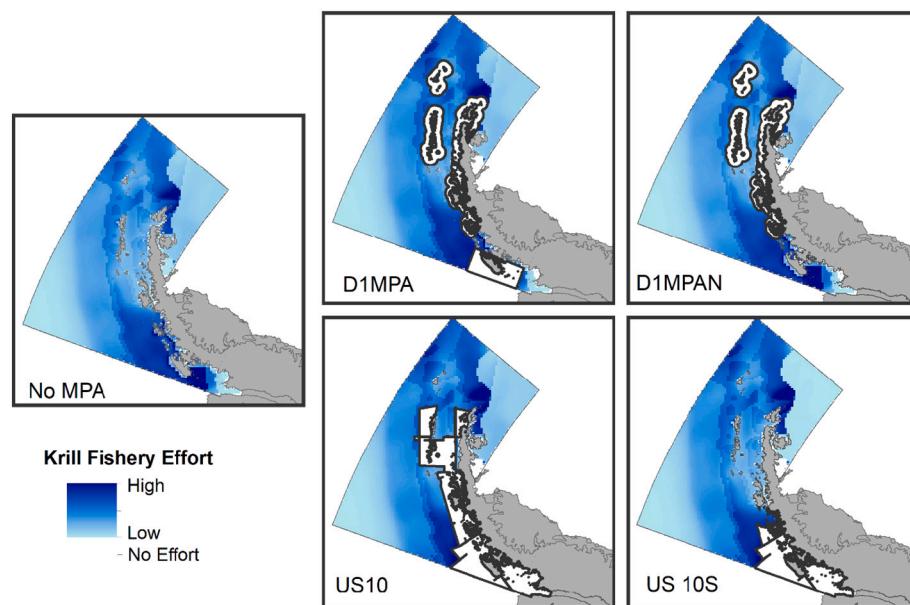


Fig. 3. Spatial distributions of fishing effort across marine protected area scenarios. Plots depict effort in December of year 20, under the decreasing ice and 5 × fishing scenarios. Darker shades of blue indicate more fishing effort, and, within the study area, white areas indicate no-take reserves in which fishing effort is absent. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

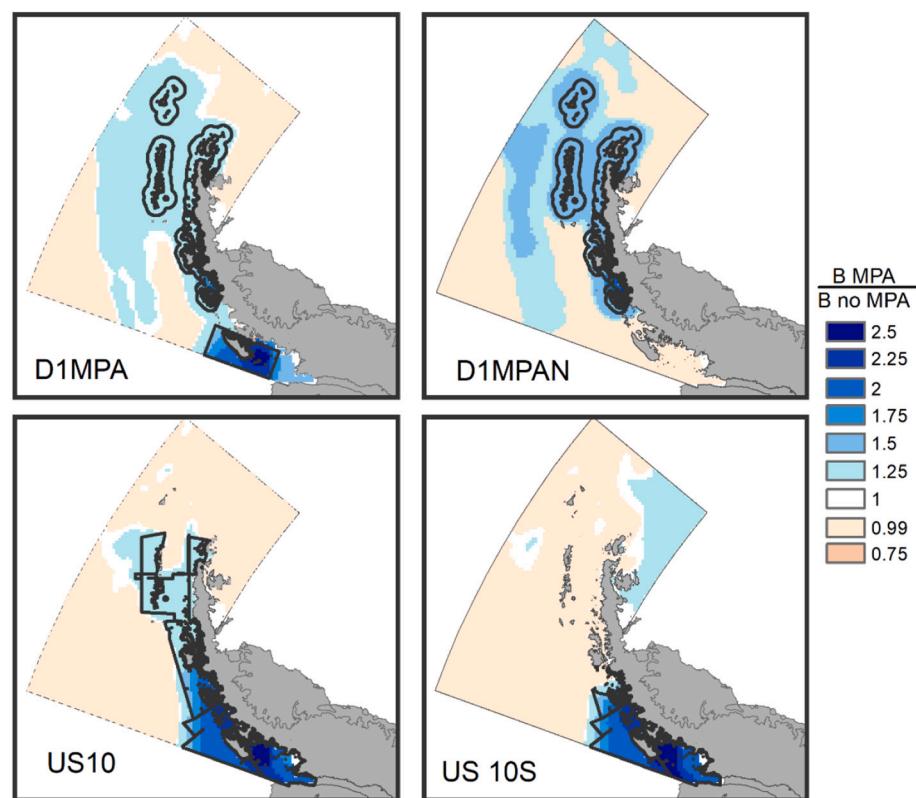


Fig. 4. Impact of marine protected areas on the biomass of krill in year 100. Plots illustrate biomass of krill given a marine protected area scenario divided by the biomass of krill with no marine protected area in place, at year 100 under the decreasing ice and 5× fishing scenarios. Salmon colors indicate declines in krill biomass, white indicates no change, and blue colors indicate increases in biomass. The darker the hue, the greater the magnitude of the impact. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

protected area could offer these species some resiliency. The D1MPA scenario displaces krill fishing away from the Bransfield Strait and around Elephant Island, areas that are important foraging grounds for gentoo and chinstrap penguins and where fur seals and penguins commonly overlap with the krill fishery (Hinke et al., 2017). To be effective, a marine protected area must cover a significantly large portion of ecologically important areas (Gaines et al., 2010; Gell and Roberts, 2003). In summary, when considering both sea-ice conditions and trophic interactions in the Western Antarctic Peninsula region, it seems that such ecologically important areas include the southern area where krill concentrate and areas near penguin and fur seal breeding colonies around the tip of the Antarctic Peninsula.

The Commission's framework for marine protected areas (CCAMLR, 2011) lists several objectives for using such areas as management tools. These objectives include protection (e.g., via no-take regulations) of biodiversity and marine habitats, populations and life-history stages, areas vulnerable to human impacts, and areas needed to maintain resilience. Our analyses indirectly address the last three objectives. The southern area of krill concentration may be vulnerable to fishing, and a no-take zone within this area could contribute to the resiliency of krill and some krill predators. Our results also highlight the importance of protecting the area around Elephant Island to improve resiliency of chinstrap penguins, and coastal areas within the Bransfield Strait to benefit gentoo penguins. The Commission makes all decisions by consensus. Thus, proposed marine protected area boundaries must be acceptable to all members of the Commission, and it seems likely that boundary configurations which simultaneously meet several of the desirable conservation objectives specified in the framework (CCAMLR, 2011) while minimizing impact on the fishery would have a greater chance of adoption.

Our results indicate that while the D1MPA scenario performed well, Adélie penguins and krill received substantial benefits solely from

protecting the southern area of krill concentration. Both species experienced the greatest benefits from the US10S scenario which protected most of this area and nothing else. The importance of this southern area to krill and Adélie penguins is further reinforced by the result indicating that neither species benefitted from the D1MPAN scenario. Less than 1% of current fishing effort and catch by the krill fishery occurs in the small scale management unit that contains the southern area of krill concentration (CCAMLR, 2018). Protection of this area could be viewed as having little or no impact on the current fishery, potentially making it politically palatable for the Commission (see Brooks, 2013). However, protection of this area alone would meet few of the objectives in the framework (CCAMLR, 2011). For example, simply protecting the southern area would not protect species that breed further north, e.g., Antarctic fur seals and *G. gibberifrons* (Kock and Jones, 2005). Further, the US10S scenario fails to protect areas known to be important to larval krill (Huntley and Brinton, 1991). On its own, the US10S scenario would not adequately protect the biodiversity of the region; the US10S scenario is too latitudinally restricted to be truly representative.

The D1MPA scenario performed best for chinstrap and gentoo penguins while also benefitting krill and Adélie penguins. The D1MPA scenario would also outperform both the US10 and US10S scenarios in terms of meeting the objectives established in the framework (CCAMLR, 2011) and in terms of projected impact on total catch. For example, the D1MPA was designed specifically to protect a representative sample of biodiversity and areas important to larval krill (Delegations of Argentina and Chile, 2017a, 2017b). By protecting a portion of the southern area of krill concentration, the D1MPA scenario contributes to resiliency for Adélie penguins and krill. However, performance of the D1MPA scenario for penguins and krill might be improved by including a larger portion of the southern area where krill concentrate.

Our model is fundamentally a food web model that considers the

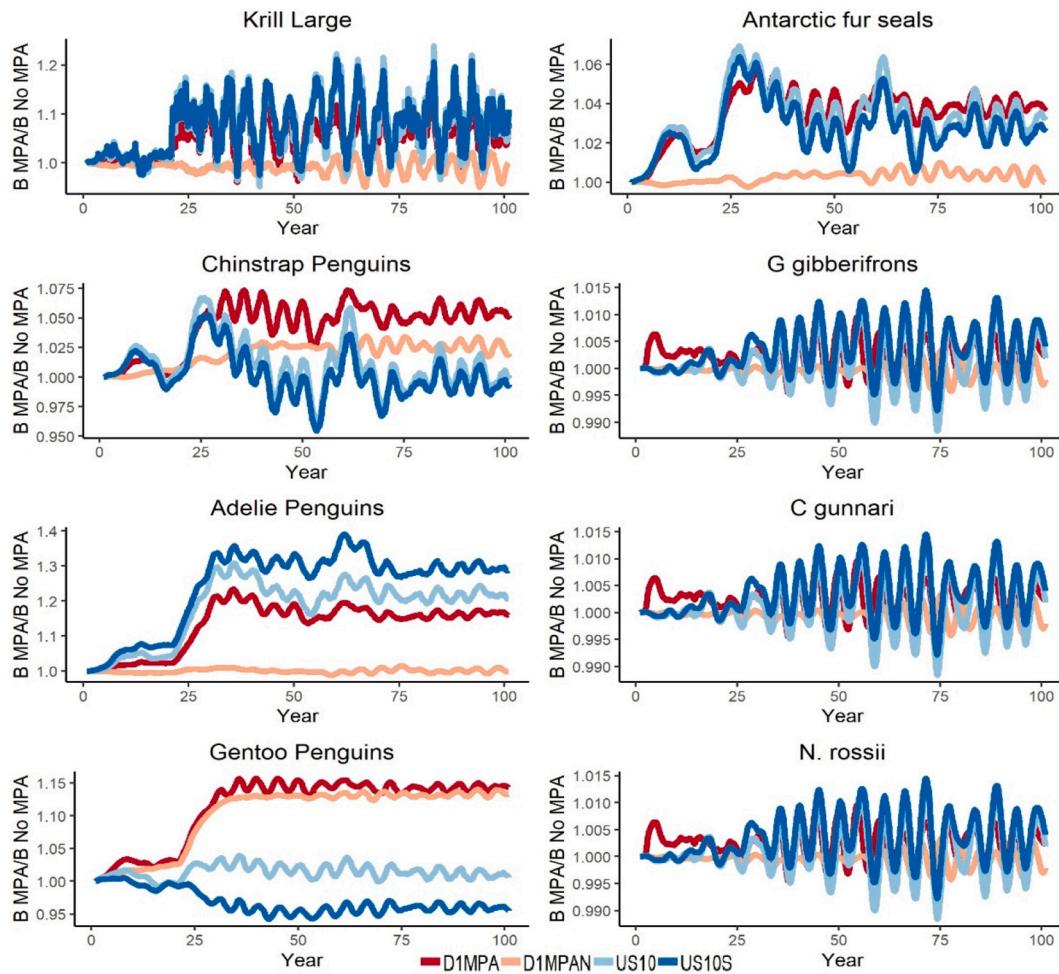


Fig. 5. Projected outcomes for the eight species used to calibrate the model. Line color indicates marine protected area scenario. Values greater than 1 indicate that the marine protected area increased biomass compared to a scenario without a marine protected area. Values less than one indicate a decrease in relative biomass and values near 1 indicate no change. All panels show results from the 5× fishing scenario.

influence of a key environmental driver, sea ice, and fishing effort, on the system dynamics. The model identified a region where krill may aggregate in the future as sea-ice loss continues, and our results indicated that establishing a no-take zone in this area drives many of the benefits of the marine protected area scenarios considered here. However, there is significant uncertainty associated with the location of where exactly krill will concentrate in the future. In our model, the locations where krill concentrate are influenced largely by sea-ice conditions and the estimated response of krill to those conditions. Sea-ice conditions were derived from those reported in 1996–2012 (Cavalieri et al., 1996, updated yearly) and may not adequately represent the more extreme losses that might result from sustained warming. We parameterized the response of krill using broad-scale trends as documented in the literature (Atkinson et al., 2019; Atkinson et al., 2004; Atkinson et al., 2009), but such an approach may not adequately reflect how krill distribution may change in response to more dramatic decreases in ice. Additionally, our model does not include directional movement of krill, which is important in determining patterns of aggregation (Richerson et al., 2015). Yet, the general trend

illustrated by our results, that the southern areas of Statistical subarea 48.1 will increase in importance as krill habitat, seems to be upheld by other investigations (Atkinson et al., 2019; Melbourne-Thomas et al., 2016). Findings from simulations run in Ecopath with Ecosim are often described as “strategic not tactical” (Link et al., 2012). It may be valuable to consider this perspective when reviewing the results of our marine protected area scenarios. In this case, it seems helpful to protect a large area where krill will aggregate in the future, while understanding that the boundaries identified here are imprecise. It may be helpful to use results from krill habitat modeling to advise on the boundaries of a marine protected area sited in Subarea 48.1.

Ecospace is only one tool that can be used to assess the potential efficacy of a candidate marine protected area. We note that the work presented here, while informative, represents the results from only a few scenarios. An additional dynamic model has been developed in the region specifically to inform for the design of a new marine protected area (Klein and Watters in press), and the proponents of the marine protected area proposed in Planning Domain 1 have also developed a static spatial model to identify boundaries (Delegations of Argentina

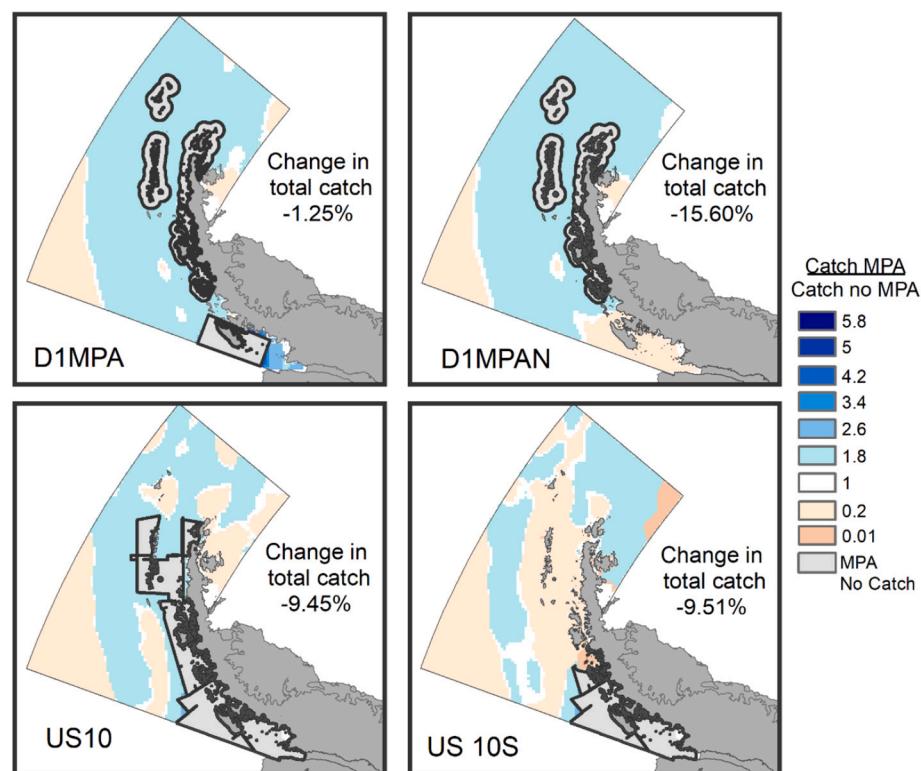


Fig. 6. Impact of marine protected areas (MPAs) on catches in year 100. Plots illustrate how the spatial location of krill catches changed with each marine protected area scenario, where catches at the end of each simulation and under each marine protected area scenario were divided by catches with no marine protected area given the decreasing ice and 5 × fishing scenarios. Salmon colors indicate declines in catch, white indicates no change, and blue colors indicate increases in catch. The darker the hue, the greater the magnitude of the impact. Impacts on total catch are indicated as percent changes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and Chile, 2017a, 2017b). Each of these models, plus that considered here, has unique strengths and weaknesses, but they could be leveraged collectively to identify a marine protected area boundary configuration that seems likely to meet several of the Commission's objectives for marine protected areas (CCAMLR, 2011).

This study demonstrates that fisheries management tools, in this case marine protected areas that act as no-take reserves, can be successfully implemented to reach conservation goals. State-of-the-art modeling allows for the inclusion of food web, fisheries and environmental considerations in spatial and temporal dynamic simulations, which is needed to evaluate the optimal placement of a protected area that can be agreed upon by various stakeholders.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

The Pew Charitable Trusts provided funds to support this work

Appendix A. Input maps

In Ecospace, habitat-capacity maps are used to describe all potential foraging areas for each modeled group (Christensen et al., 2014). Habitat-capacity maps are used to calculate foraging capacity by using spatial forcing functions and species-specific response curves to estimate the cumulative impact of multiple environmental drivers (Christensen et al., 2014). Sufficient data are lacking to draw response curves for many potential environmental drivers. To reduce uncertainty associated with drawing response curves, we used distribution maps based on sightings data and

under contract # 31815. Much of the work conducted for this study was as part of a doctoral dissertation and one of the authors (AD) received financial support from the Department of Environmental Science and Policy at George Mason University to develop the model. We thank C. Reiss, J. Hinke, M. Goebel, C. Jones, A. Cossio, J. Walsh, M. Santos and A. Capurro for providing data and insight that contributed to this study. We thank J. Buszowski and J. Steenbeek for assistance in using Ecospace and the external data framework. We would like to thank the reviewers and editors for their thoughtful review and feedback on our manuscript.

CRediT authorship contribution statement

Adrian Dahood: Conceptualization, Methodology, Formal Analysis, Data Curation, Writing – Original Draft, Visualization, Funding acquisition. **Kim de Mutsert:** Methodology, Writing – Review & Editing, Supervision, Funding acquisition. **George M. Watters:** Methodology, Writing - Review & Editing, Supervision.

known foraging locations as a proxies for habitat capacity. By entering maps directly into the habitat capacity-module, the model was effectively constrained as to where it could allocate biomass. For each map, every cell was initially assigned a value between zero and one to distinguish the quality of the habitat. Cells scored as zero could, however, acquire a positive value over the course of simulations in response to environmental drivers. For simplicity and consistency, all maps entered into the habitat-capacity module will be referred to as foraging-area maps. A foraging-area map was drawn for each consumer species or functional group. When available, maps were based on sightings or tracking data, and higher value areas represent locations where animals have been observed to concentrate for foraging. If no such data were available, maps were based on bathymetry. The data that informed these foraging-area maps are presented in Table A1, the maps are shown below (Figs. A1-A7).

Table A1
Sources for foraging area maps.

Group name	Foraging area map source
Killer whales	B. Pitman (Pers. Comm. March 2015), Second WS-MPA Domain 1 (2015)
Leopard seal	D. Krause (Pers. Comm. March 2015), Burns et al. (2004) ; Burns et al. (2008) , Forcada et al. (2012) , Friedlaender et al. (2011) , Meade et al. (2015)
Weddell seal	D. Krause (Pers. Comm. March 2015), Burns et al. (2004) ; Burns et al. (2008) , Forcada et al. (2012) , Friedlaender et al. (2011) , Meade et al. (2015)
Crabeater seal	D. Krause (Pers. Comm. March 2015), Burns et al. (2004) ; Burns et al. (2008) , Forcada et al. (2012) , Friedlaender et al. (2011) , Meade et al. (2015)
Antarctic fur seals	D. Krause and M. Goebel (Pers. Comm. March 2015), Second WS-MPA Domain 1 (2015)
S elephant seals	Costa et al. (2010) ; Hückstädt et al. (2012) , Second WS-MPA Domain 1 (2015)
Sperm whales	Carbotte et al. (2007) ; Taylor et al. (2008) ; Whitehead (2003)
Blue whales	Kemp and Bennett (1932)
Fin whales	C. Reiss and J. Santorra (Pers. Comm. March 2015)
Minke whales	A. Friedlaender (Pers. Comm. April 2017), Second WS-MPA Domain 1 (2015)
Humpback whales	A. Friedlaender (Pers. Comm. April 2017), Second WS-MPA Domain 1 (2015)
Emperor penguins	Kirkwood and Robertson (1997) ; Wienecke and Robertson (1997) , Second WS-MPA Domain 1 (2015)
Gentooo penguins	J. Hinke (Pers. Comm. March 2015), Second WS-MPA Domain 1 (2015)
Chinstrap penguins	J. Hinke (Pers. Comm. March 2015), Hinke et al. (2015) , Second WS-MPA Domain 1 (2015)
Adélie penguins	J. Hinke (Pers. Comm. March 2015), Hinke et al. (2015) , Erdmann et al. (2011) Second WS-MPA Domain 1 (2015)
Macaroni penguins	Bost et al., 2009 ; Green et al. (2005) ; Naveen and Lynch (2011)
Flying birds	This species group is large and diverse, the foraging area was not constrained in the model
Cephalopods	This species group is large and diverse, the foraging area was not constrained in the model
Myctophids (off shelf)	Hill et al. (2007) defined off-shelf waters as deeper than 500 m
On-shelf fish	Hill et al. (2007) defined shelf waters as shallower than 500 m
<i>N. rossii</i>	DeWitt et al. (1990)
C. gunnari	Iwami and Kock (1990) Kock and Jones (2005)
G. gibberifrons	Iwami and Kock (1990) Kock and Jones (2005)
Salps	Pers. Comm., Christian Reiss, NOAA-AMLR, March 2015, Second WS-MPA Domain 1 (2015)
Benthic invertebrates	Gutt et al. (2013) ; Lockhart and Jones (2008)
Large krill	Second WS-MPA Domain 1 (2015)
Small krill	Second WS-MPA Domain 1 (2015) , Frazer et al. (2002) , Huntley and Brinton (1991) , Pakhomov et al. (2004) , Ashjian et al. (2008) , Siegel et al. (2013)
Other euphausiids	Fisher et al. (2004) Pers. Comm., Christian Reiss, NOAA-AMLR, March 2015, (Second WS-MPA Domain 1, 2015)
Microzooplankton	This species group is large and diverse, the foraging area was not constrained in the model
Mesozooplankton	This species group is large and diverse, the foraging area was not constrained in the model
Macrozooplankton	This species group is large and diverse, the foraging area was not constrained in the model
Small phytoplankton	This species group is large and diverse, the foraging area was not constrained in the model
Large phytoplankton	This species group is large and diverse, the foraging area was not constrained in the model
Ice algae	Area was not constrained, but ice algae were given a linear (slope of 1) response to the dynamic sea-ice maps. This limited ice algae to cells that had ice in them.

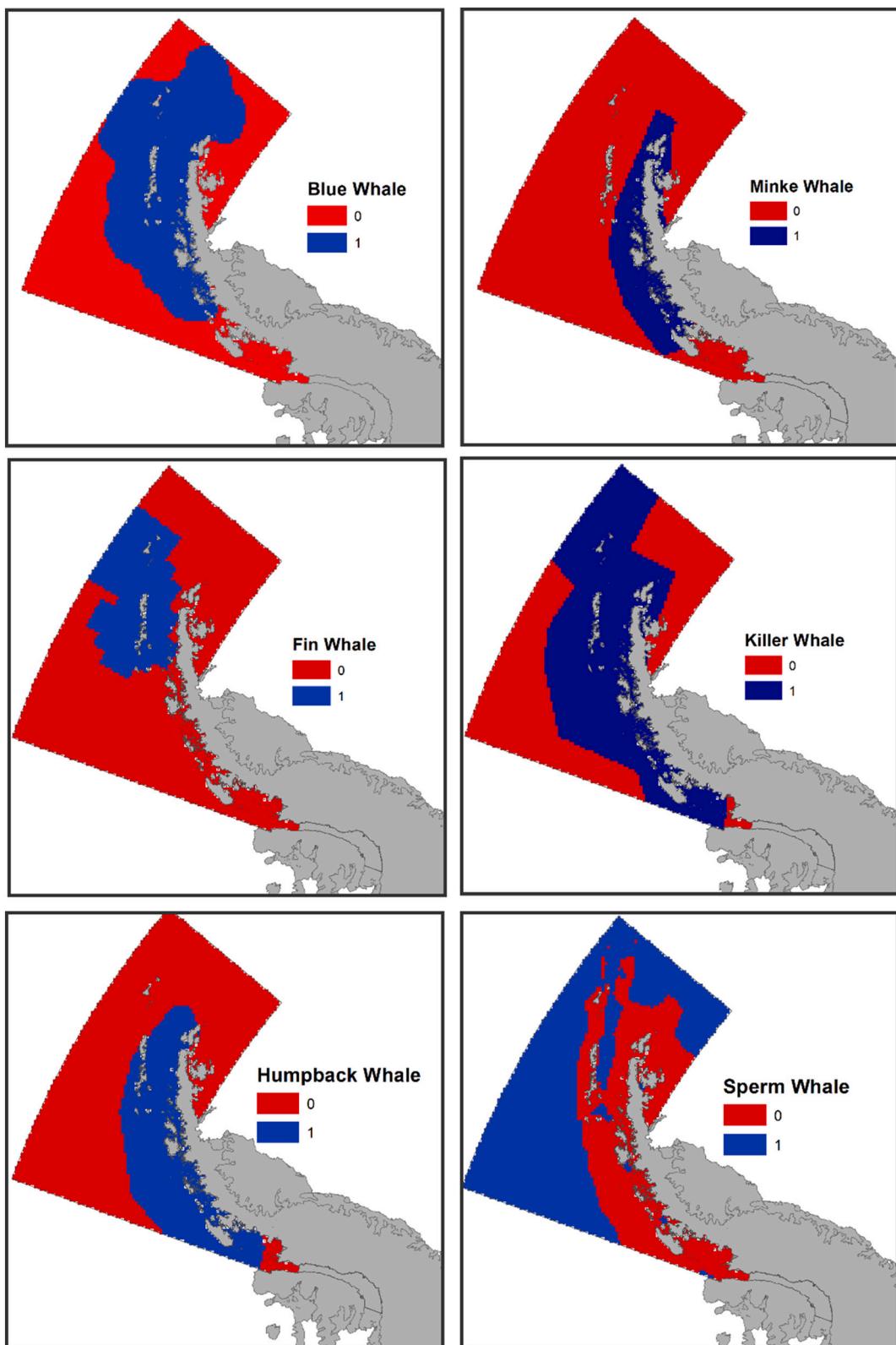


Fig. A1. Cetacean foraging areas. Blue denotes available foraging areas. Red denotes areas not available for foraging. For cetaceans all available foraging areas are considered equally good, and were assigned the value of 1.

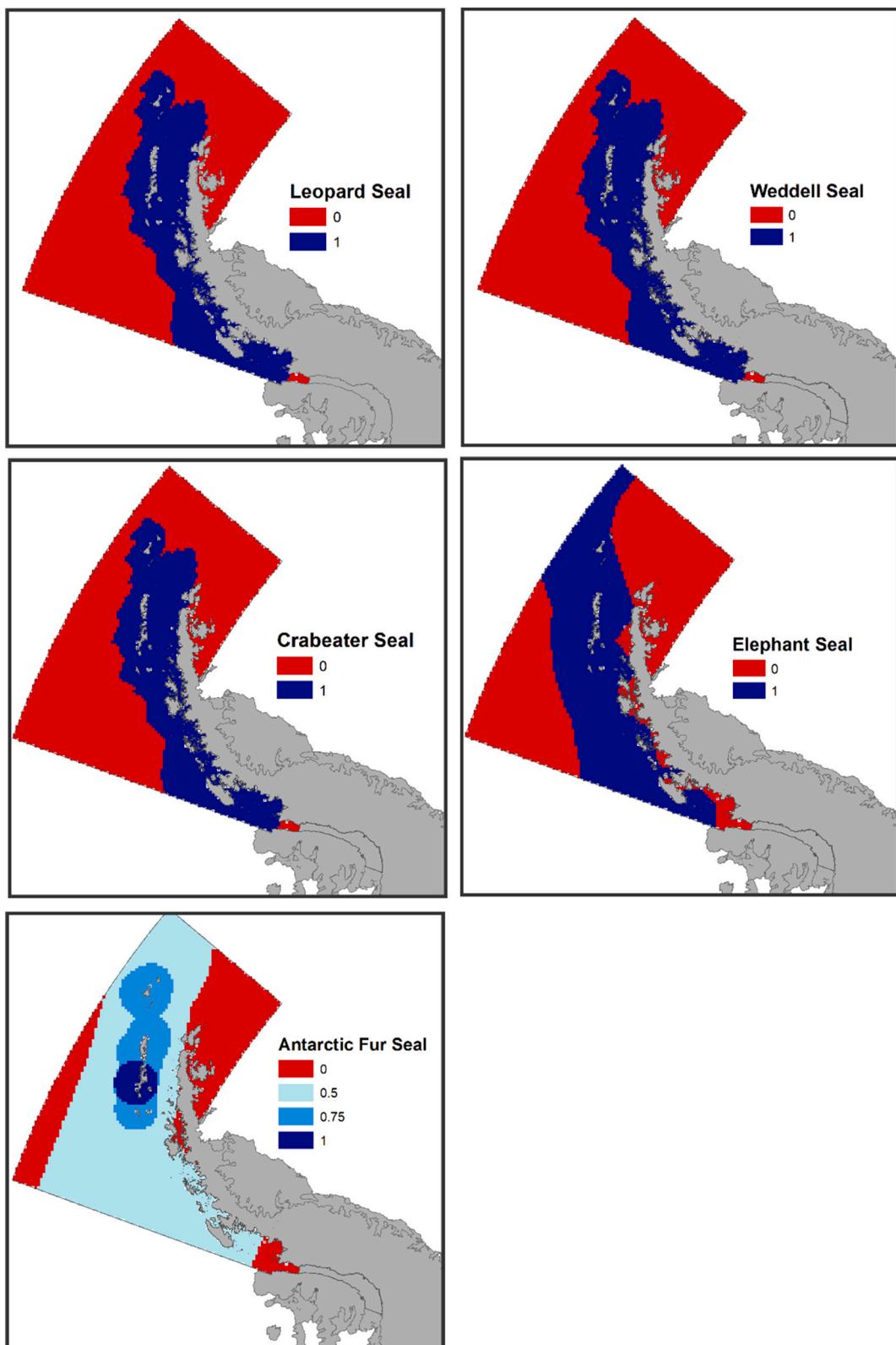


Fig. A2. Foraging areas for pinnipeds. For leopard, Weddell, crabeater, and Elephant seals, blue denotes available foraging areas and red denotes areas not available for foraging. For Antarctic fur seals, the region around Cape Shirreff where approximately 80% of the fur seal population in the Western Antarctic Peninsula breed, is depicted in dark blue (value = 1). Areas around smaller fur seal colonies are shown in medium blue (value = 0.75) (Goebel and Reiss, 2014). Areas where tagged fur seals have been observed are shown in light blue (value = 0.50). Areas that are presumed not to be highly utilized by foraging fur seals, are shown in red (value = 0).

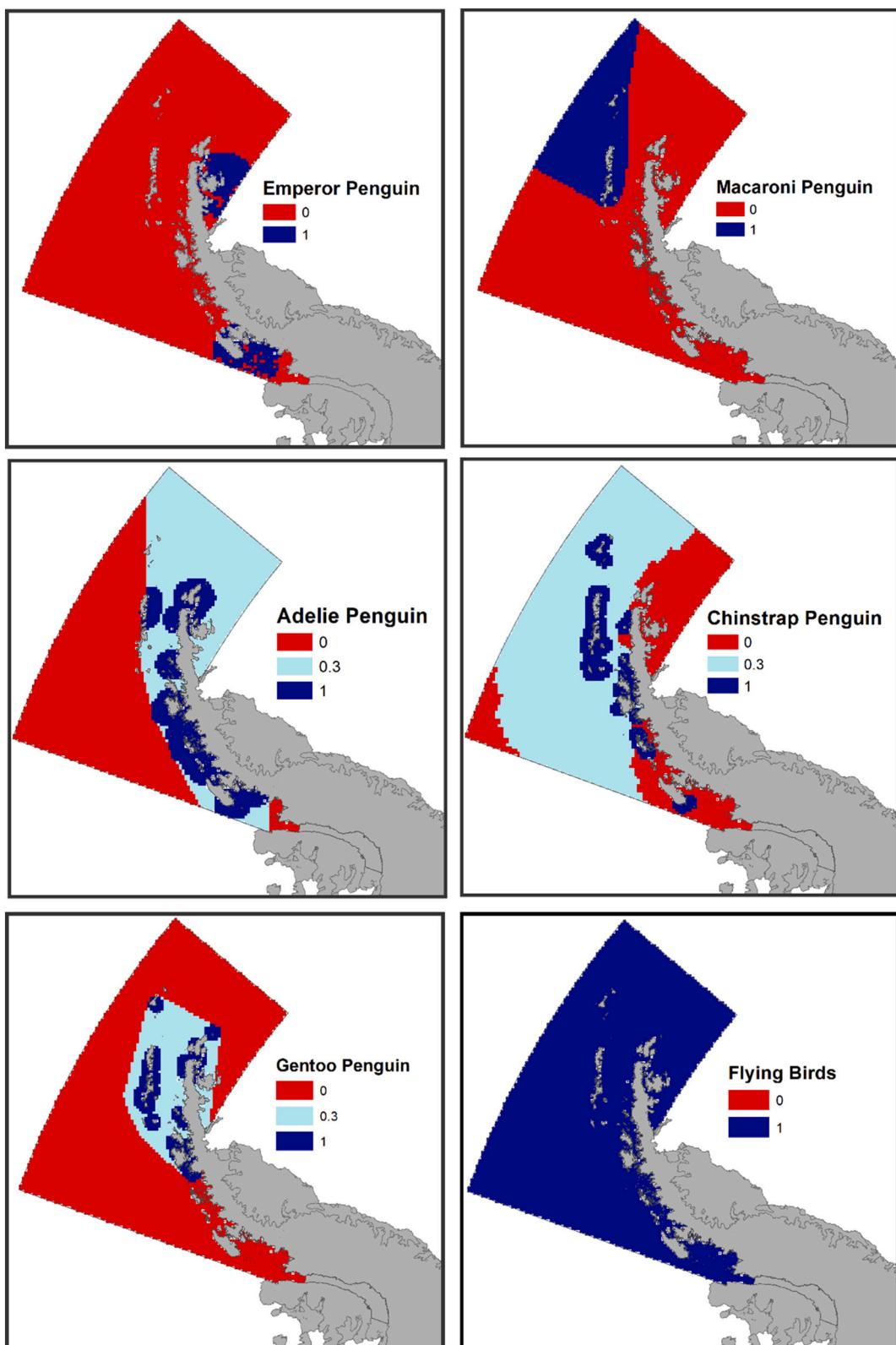


Fig. A3. Foraging areas for birds. Blue denotes available foraging areas. Red denotes areas not available for foraging (value = 0). For Adélie, chinstrap, and gentoo penguins, areas near known penguin colonies are shown in dark blue (value = 1). Additional areas where penguins have been tracked in the winter are shown in medium blue (value = 0.3). Areas where penguins have not been tracked, and are presumed not to be utilized by foraging penguins, are shown in red (value = 0). The foraging area for flying birds was not constrained, and all cells were assigned a value of 1.

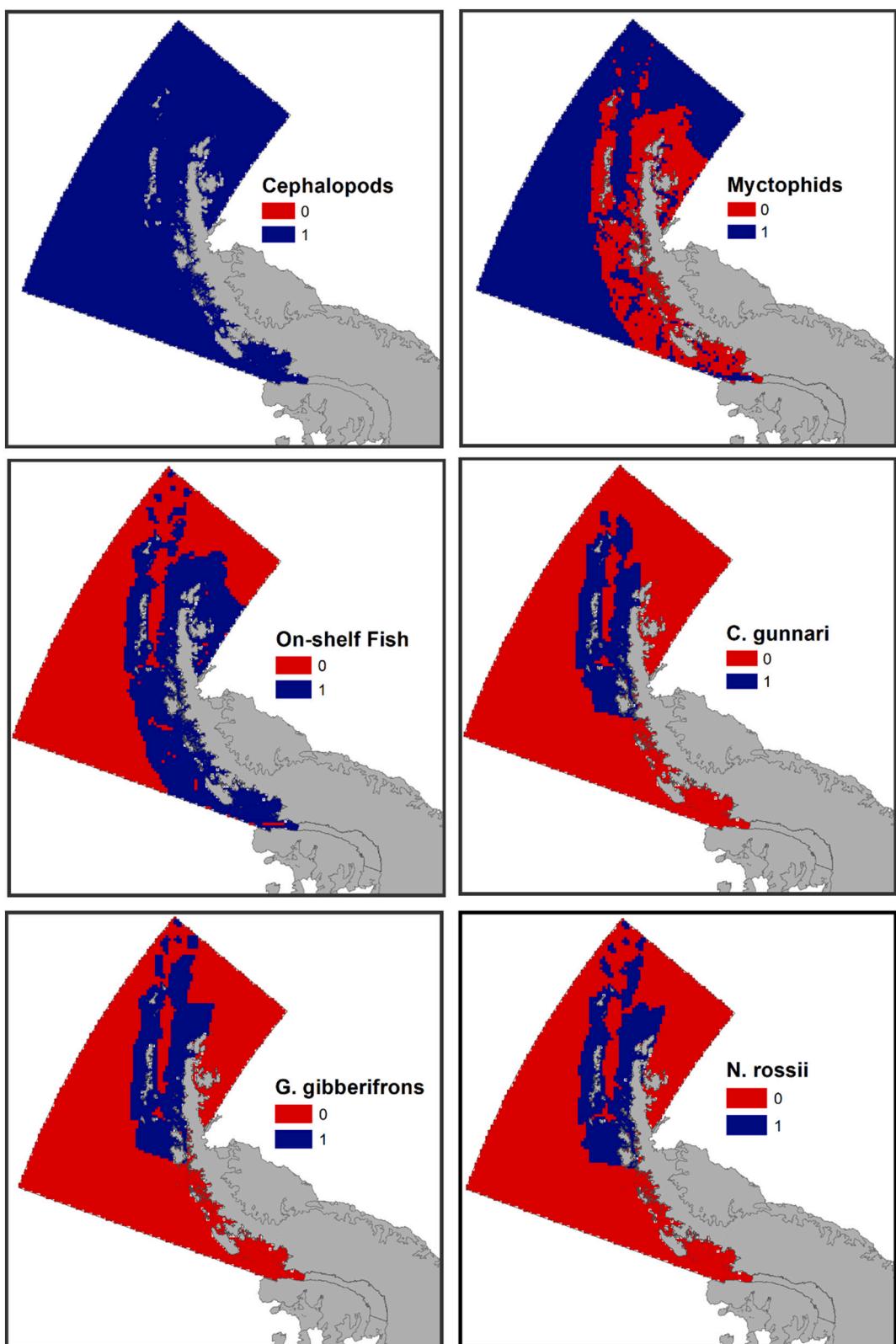


Fig. A4. Foraging areas for cephalopods and fishes. Blue denotes available foraging areas. Red denotes areas not available for foraging. The foraging area for cephalopods was not constrained and all cells were assigned a value of 1.

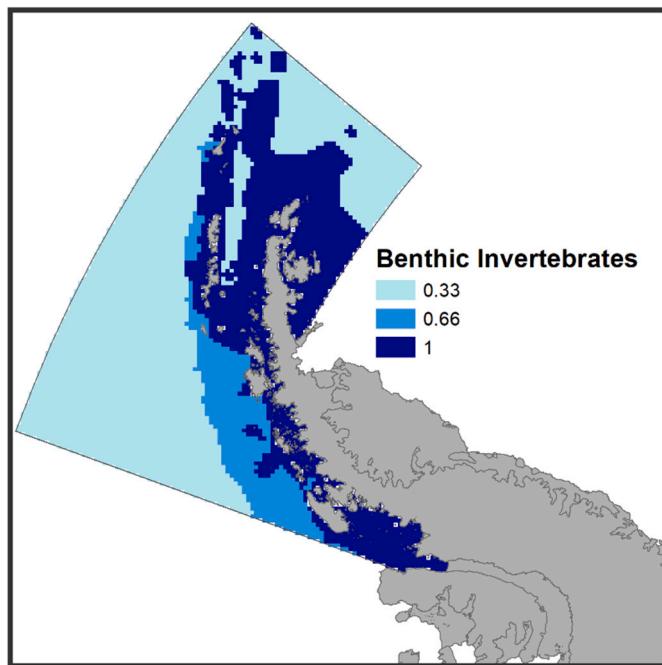


Fig. A5. Foraging areas for benthic invertebrates. Following the work of [Lockhart and Jones \(2008\)](#), dark blue (value = 1) denotes areas that are shallower than 800 m and cooler than 1 °C, which are expected to have the highest abundance of benthic invertebrates. Medium blue (value = 0.66) denotes areas that are shallower than 800 m and warmer than 1 °C, which are expected to have a moderate abundance of benthic invertebrates. Light blue (value 0.33) denotes areas deeper than 800 m, which are expected to have a low abundance of benthic invertebrates.

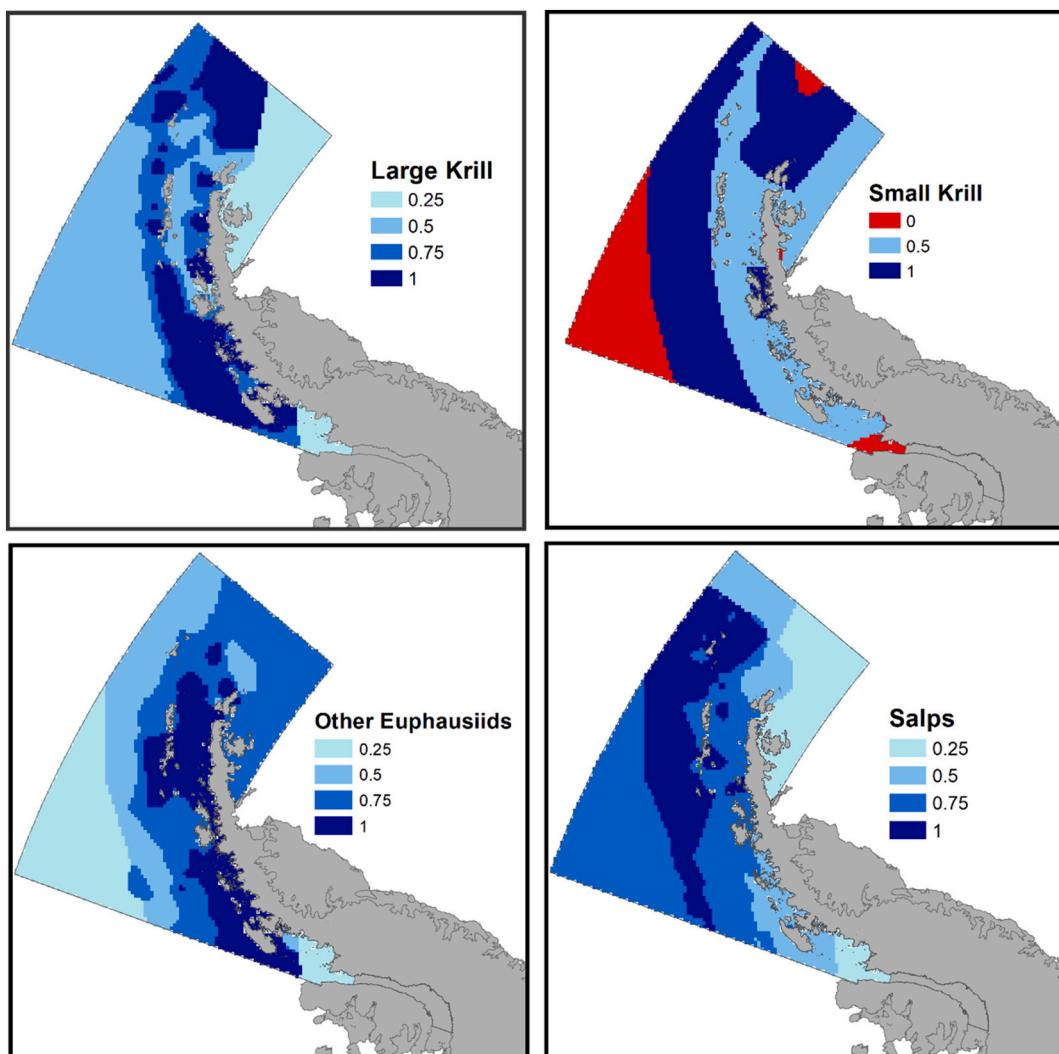


Fig. A6. Foraging areas for large krill, small krill, other euphausiids, and salps. Potential foraging areas were split into four bins (shown in shades of blue) based on estimates from zooplankton surveys. Areas that had the highest density of animals were assumed to be the highest quality foraging areas and were colored dark blue (value = 1). Areas with moderate (value = 0.75) and low (value = 0.5) density of animals. Light blue (value = 0.25) indicates areas that were not well sampled; the value of 0.25 recognizes that some mature zooplankton likely occur in those waters.

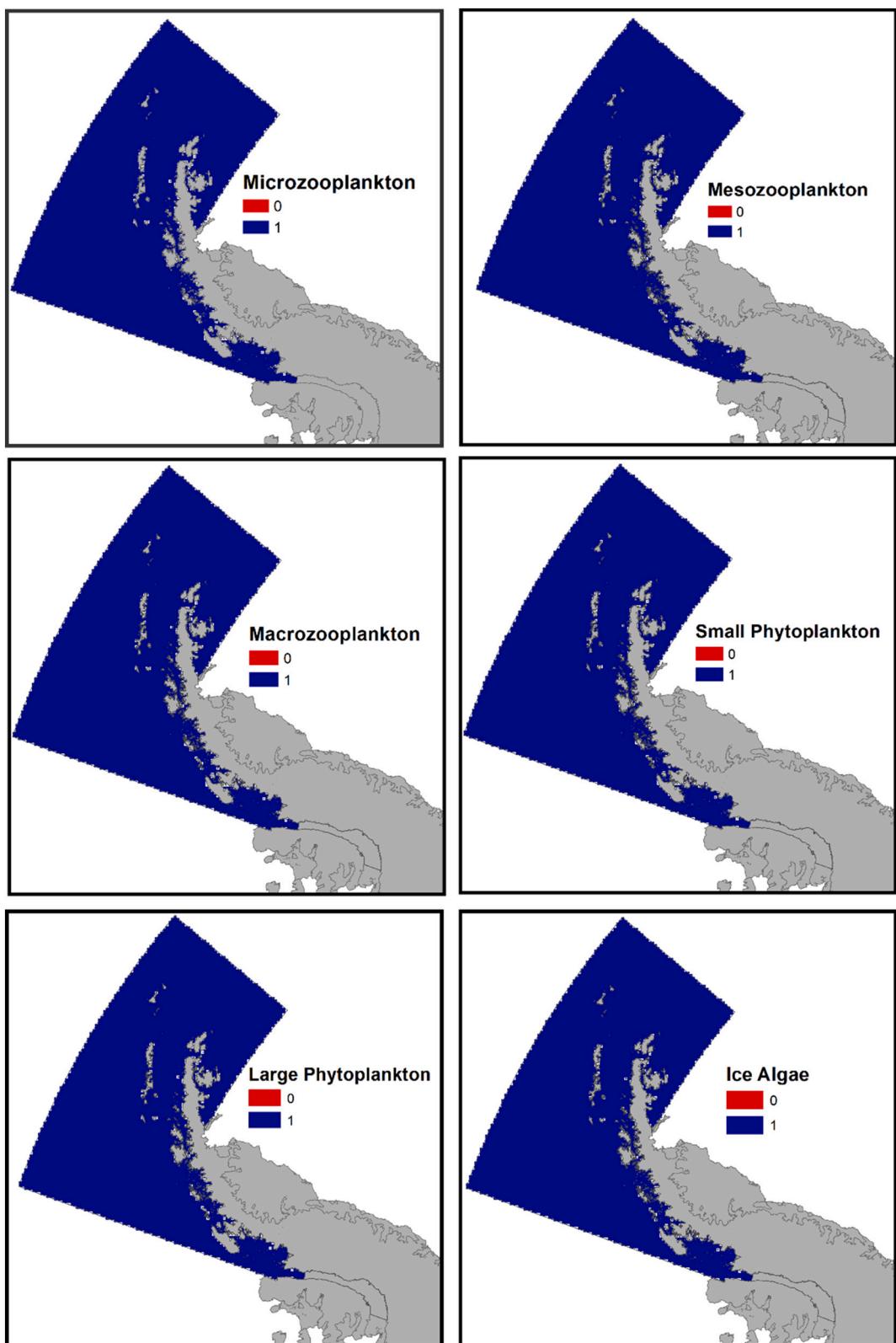


Fig. A7. Foraging areas for various other plankton. These groups were not constrained and all cells were assigned a value of 1.

Appendix B. Dispersal

In Ecospace, movement rates across cell boundaries are related to annual movement distances (Martell et al., 2005; Walters et al., 1999). Movement rates, M_i , were calculated from swim speeds to estimate the proportion of biomass exiting any given cell, assuming that movement is random (Martell et al., 2005). Following Martell et al. (2005) the following equation was used to calculate M_i which was entered as the base dispersal rate.

$$M_i = \frac{S_i}{\pi L} \quad (B1)$$

S_i is the swim speed (or current speed for plankton) and L is the length of the side of the cell (nominally 10 km). The sources for swim speeds and resulting base dispersal rates are provided in Table B1.

Dispersal speed varies across space (Christensen et al., 2014); M_i is simply the starting value. Ecospace uses a “habitat gradient function” that interacts with the habitat-capacity module and indicates higher rates of movement out of less suitable cells (Christensen et al., 2014). In effect, this function directs biomass into cells identified with higher values in the foraging-area maps, but does not allow users to specify a directional pattern of movement.

Table B1
Dispersal speeds.

Name	Swim speed source	Swim speed m/s	Base dispersal km/yr
Killer whales	Williams and Noren (2009)	1.6	1606.32
Leopard seal	Rogers et al. (2005)	1.2	1204.74
Weddell seal	Davis et al. (1999)	1.2	1204.74
Crabeater seal	Adam (2005); Bengtson et al. (1993); Nordøy et al. (1995)	1.2	1204.74
Antarctic fur seals	Watanabe et al. (2011)	1.72	1726.79
S elephant seals	Watanabe et al. (2011), Horsburgh et al. (2008)	1.3	1305.13
Sperm whales	Watanabe et al. (2011)	1.7	1706.71
Blue whales	Watanabe et al. (2011)	2.23	2238.81
Fin whales	Watanabe et al. (2011)	2.4	2409.48
Minke whales	Motani (2002)	3.2	3212.64
Humpback whales	Watanabe et al. (2011)	1.45	1455.73
Emperor penguins	Watanabe et al. (2011)	2.14	2148.45
Gentooo penguins	Watanabe et al. (2011)	2.3	2309.08
Chinstrap penguins	Watanabe et al. (2011)	2.3	2309.08
Adélie penguins	Watanabe et al. (2011)	2	2007.90
Macaroni penguins	Watanabe et al. (2011)	2	2007.90
Flying birds	Watanabe et al. (2011)	1.4	1405.53
Cephalopods	O'Dor (2002)	0.2	200.79
Myctophids (off shelf)	Estimated with Sambilay (1990) and Fishbase	0.1	100.39
On-shelf fish	Estimated with Sambilay (1990) and Fishbase	0.13	130.51
N. rossii	Estimated with Sambilay (1990) and Fishbase	0.14	140.55
C gunnari	Estimated with Sambilay (1990) and Fishbase	0.13	130.51
G gibberifrons	Estimated with Sambilay (1990) and Fishbase	0.13	130.51
Salps	Fahrbach et al. (1992)	0.1	100.39
Benthic invertebrates	Fahrbach et al. (1992)	0.05	50.20
Large krill	Tarling and Thorpe (2014)	0.2	200.79
Small krill	Fahrbach et al. (1992)	0.1	100.39
Other euphausiids	Fahrbach et al. (1992)	0.1	100.39
Microzooplankton	Fahrbach et al. (1992)	0.1	100.39
Mesozooplankton	Fahrbach et al. (1992)	0.1	100.39
Macrozooplankton	Fahrbach et al. (1992)	0.1	100.39
Small phytoplankton	Fahrbach et al. (1992)	0.1	100.39
Large phytoplankton	Fahrbach et al. (1992)	0.1	100.39
Ice algae	Fahrbach et al. (1992)	0.1	100.39
Detritus	Fahrbach et al. (1992)	0.1	100.39

Appendix C. Model tuning

To tune the spatio-temporal simulations in Ecospace, sea-ice concentration was used to influence patterns of species distribution and abundance. The spatio-temporal framework, which allows maps of environmental data to be fed into the model at each time step (Steenbeek et al., 2013), was used to include monthly maps of average sea-ice concentration (Cavalieri et al., 1996, updated yearly, accessed through the U.S. National Snow and Ice Data Center).

Functional response curves were used to describe how species respond to spatio-temporal patterns in sea-ice concentration. Response curves were evaluated for the years 1996–2012, using sightings data and reported trends in abundance as reference. Attempts to draw curves representing a negative response to sea ice-concentration were unsuccessful in Ecospace, so maps of open water concentration (the inverse of sea-ice concentration) were made. A positive response to either sea ice or open water conditions was assigned based on documented foraging strategies and curves were applied to a limited number of model groups (Table C1).

Table C1

Modeled responses to variations in sea-ice concentration.

Model group	Positive response to	Source
Antarctic fur seal (<i>Arctocephalus gazella</i>)	Sea ice	Goebel and Reiss (2014)
Adélie penguin (<i>Pygoscelis adeliae</i>)	Sea ice	Hinke et al. (2014); Lynch et al. (2012); Trivelpiece et al. (2011)
Chinstrap penguin (<i>Pygoscelis antarcticus</i>)	Sea ice	Lynch et al. (2012); Trivelpiece et al. (2011)
Krill (<i>Euphausia superba</i>)	Sea ice	Atkinson et al. (2004); Atkinson et al. (2009)
<i>Gobionotothen gibberifrons</i>	Sea ice	Dahood et al. (2019)
Ice algae	Sea ice	This group is defined as living in sea ice
Humpback whale (<i>Megaptera novaeangliae</i>)	Open water	Friedlaender et al. (2011), A. Friedlaender (Pers. Comm April 2017)
Sperm whale (<i>Physeter macrocephalus</i>)	Open water	Taylor et al. (2008)
Gentooo penguin (<i>Pygoscelis papua</i>)	Open water	Forcada et al. (2006); Hinke et al. (2007)
Macaroni penguin (<i>Eudyptes chrysophthalmus</i>)	Open water	Gorman et al. (2010)
<i>Champscephalus gunnari</i>	Open water	Iwami and Kock (1990)
<i>Notothenia rossi</i>	Open water	DeWitt et al. (1990)
Salps (e.g. <i>Salpa thompsonii</i>)	Open water	Atkinson et al. (2004)
Other euphausiids (<i>Euphausia crystallorophias</i> and <i>Thysanoessa macrura</i>)	Open water	Fisher et al. (2004)

While the literature describes generalized responses to ice conditions for some species, no detailed response curves for sea-ice concentration are available. Several response curves were tested, but, ultimately, only variations of a linear response were retained in the model. The retained curves and the species to which they were applied are illustrated in Figs. C1 and C2. Two examples of the tuning process, one for a positive response to sea-ice concentration (Adélie penguins) and one for a positive response to open water conditions (salps) are also provided below.

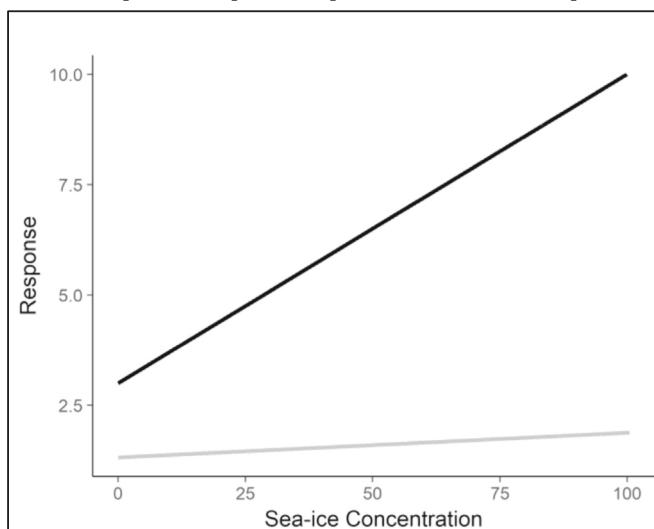


Fig. C1. Retained sea-ice response curves. The steeper line (black) was applied to fur seals, chinstrap penguins, Adélie penguins, *G. gibberifrons*, Large Krill and Small Krill. The less steep line (grey) was applied to ice algae. The response value (y-axis) is a multiplier that is applied to cells (Christensen et al., 2014) and draws biomass of the groups to which it was applied into cells with higher sea-ice concentration.

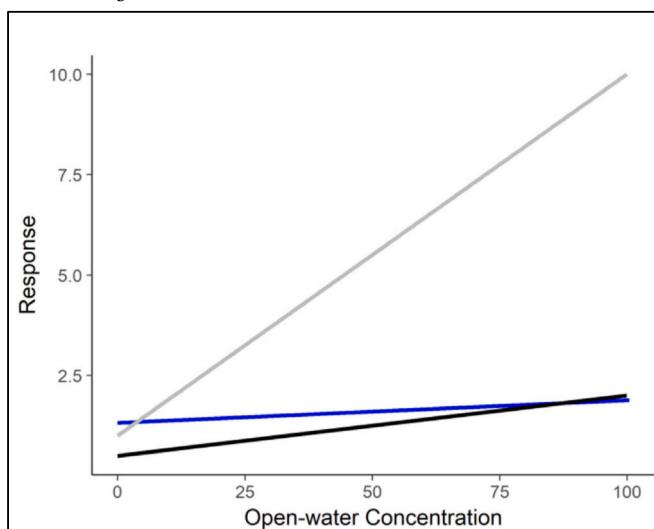


Fig. C2. Retained open water response curves. The steeper line (grey) was applied to Gentoo Penguins and *C. gunnari*. The blue line was applied to salps. The black

line was applied to Sperm Whales, Humpback Whales, Macaroni Penguins, N. rossii and Other Euphausiids. The response value (y-axis) is a multiplier that is applied to cells (Christensen et al., 2014) and draws biomass of the groups to which it was applied into cells with greater open-water concentration.

Adélie penguin populations respond to changes in sea-ice conditions (Croxall et al., 2002; Hinke et al., 2014; Jenouvrier et al., 2005) and prefer foraging near and in pack ice, where ice concentration is at least 15% (Fraser et al., 1992; Trivelpiece et al., 2011). Two sea-ice response curves were tested for Adélie penguins (Fig. C3A), and both had similar effects on total Adélie penguin biomass (Fig. C3B). In the first, Adélie penguins responded positively when there was greater than 15% sea-ice concentration and had no response to lower ice concentrations. The use of this curve resulted in the elimination of Adélie penguins from still occupied colonies prior to 2012 (Fig. C3C). Adélie penguins have high site fidelity (Trivelpiece et al., 1987), and will return to their natal colonies regardless of local ice conditions. A linear positive response to sea ice may be a biologically more appropriate response curve. Use of a linear response curve resulted in known penguin colonies persisting, but more northern colonies decreasing in relative importance during the model run (Fig. C3D). This result mimics what has been observed in the region (Lynch et al., 2012). The linear response curve was retained in the model.

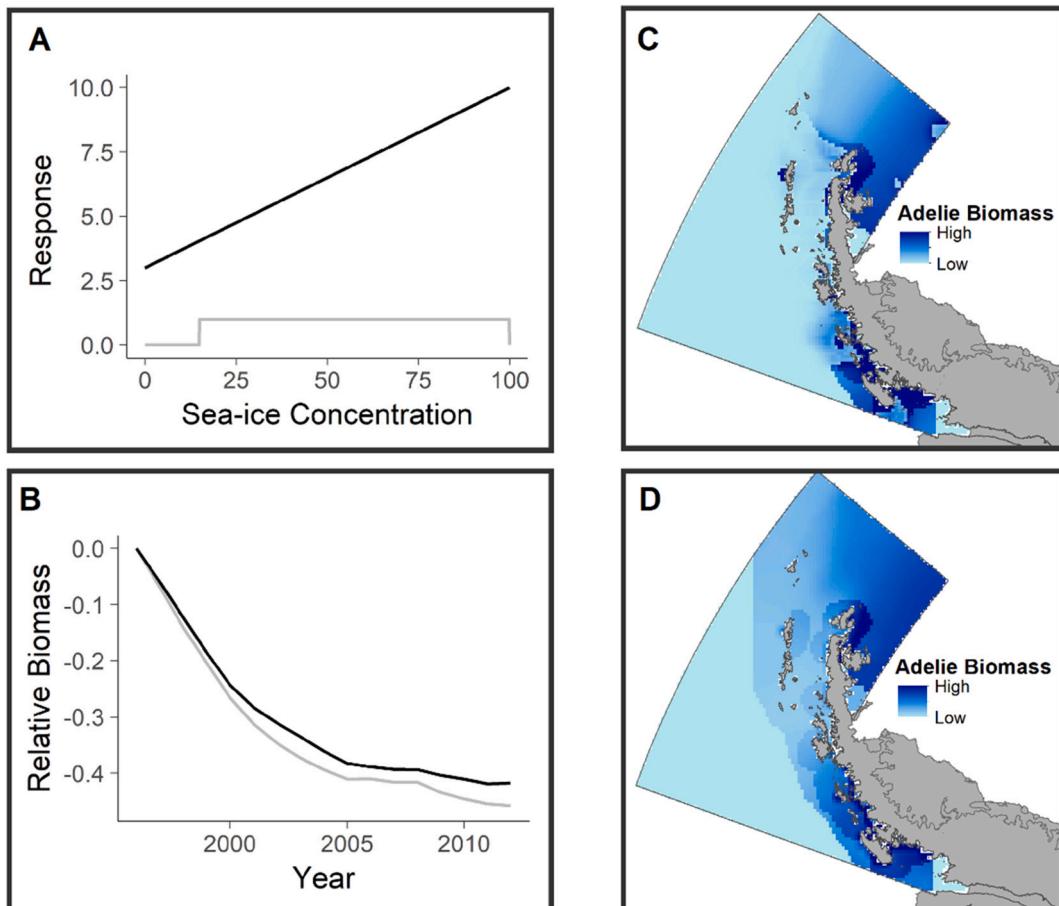


Fig. C3. Spatial response curves tested for Adélie Penguins. Two curves describing Adélie penguin response to sea-ice concentration were tested in Ecospace (A), a curve where there is no response until 15% concentration (grey), and a linear response (black). Regardless of the curve used, the temporal biomass accumulation pattern was similar, though the linear (black) curve resulted in more biomass in the system (B). The largest difference in the curves was the spatial distribution of biomass. Use of the threshold response resulted in the abandonment of still occupied colonies in the South Shetland Islands (C). The linear response curve resulted in a spatial distribution where all currently occupied colonies remained occupied (D).

Salps, specifically *Salpa thompsoni*, are an important open water pelagic zooplankton that are increasing in abundance (Atkinson et al., 2004; Atkinson et al., 2009). Initial implementation of the Ecospace simulation without using open water concentration as an environmental driver indicated the opposite pattern. To correct this, two increasing, linear responses to open water concentrations were evaluated (Fig. C4A). While the slope of the line significantly impacted relative biomass (Fig. C4B), there was very little difference in spatial distribution of salps (Fig. C4C and D). Using the steep linear response resulted in significant growth in the relative biomass of salps and caused crashes in mesozooplankton. The flatter curve that yielded the more moderate relative biomass increase was retained in the model.

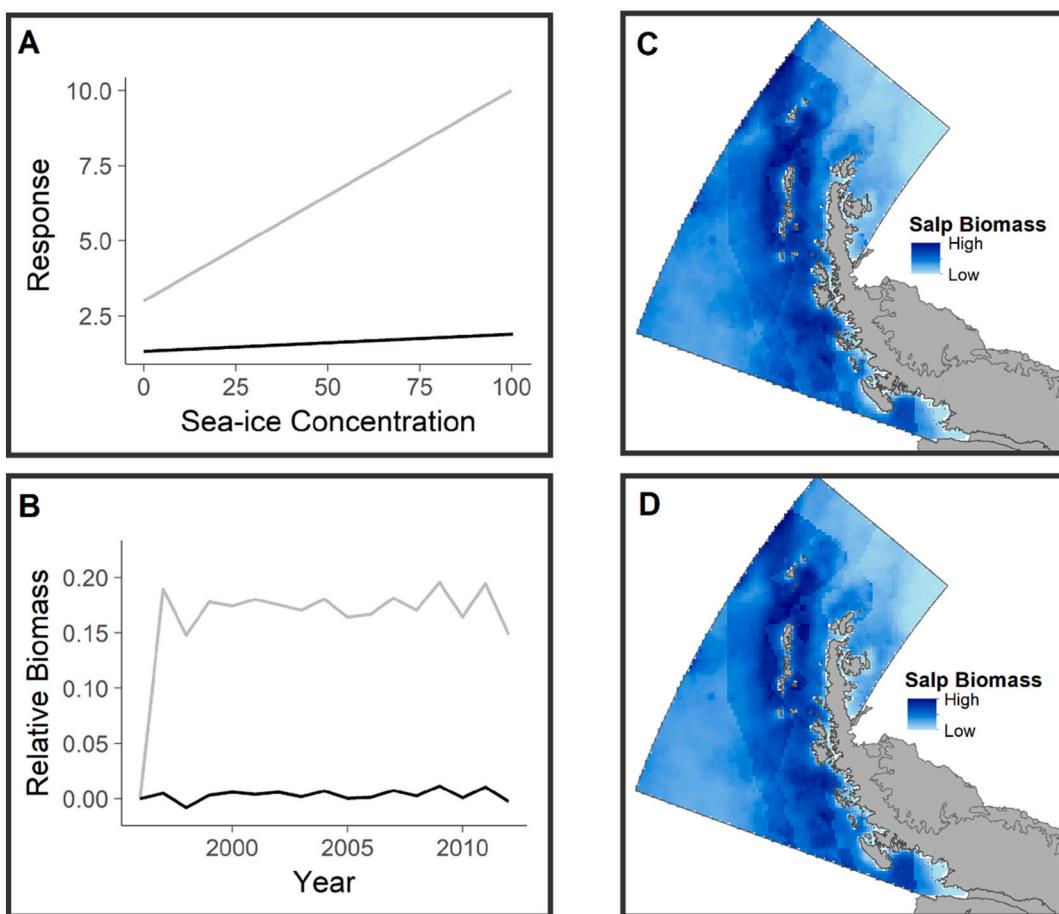


Fig. C4. Spatial response curves tested for salps. Two curves were tested to describe salp response to open water (A). Relative log Biomass outcomes varied significantly between curves with the steeper (grey) curve resulting in much higher biomass (B), but spatial distribution patterns were similar (C grey curve and D black curve). The flatter (black) curve was retained.

Appendix D. Formulation of sea-ice scenarios

It is widely acknowledged that sea ice in the Antarctic Peninsula region drives ecosystem patterns, is rapidly changing, and is expected to decrease in future years (Ducklow et al., 2007; Ducklow et al., 2013; Martinson et al., 2008; Vernet et al., 2008). However, good, spatially-explicit predictions of sea-ice concentration are not currently available. Therefore, we conducted a sensitivity analysis using two possible sea-ice scenarios: one in which conditions stayed the same as they were during 1996–2012, and a second scenario in which sea-ice concentration decreased. To create both scenarios, the seventeen years of sea-ice data used in the Ecosim and Ecospace simulations were resampled to build 100-year spatially and temporally explicit time series. Each year of data was classified into one of four bins, based on the sea-ice index that was developed for the Ecosim simulations (Dahood et al., 2019). The sea-ice index was based on the average area (km^2) of minimum summer sea ice. An index value greater than one indicates years for which the minimum summer sea-ice area was greater than average; value less than 1 indicate below average sea-ice area (Dahood et al., 2019). Bins were defined using natural breaks in the data (Table D1).

Table D1
Sea-ice index bins.

Bin #	Years	Sea-ice index value range
0	1999, 2001, 2004, 2007, 2008	0.0228–0.0918
1	2009, 2010, 2011	0.1566–0.1926
2	1997, 1998, 2000, 2003, 2012	0.4321–1.1541
3	1996, 2002, 2006, 2005	1.9773–4.9426

Two different 100-year duration sea-ice scenarios were created. Both scenarios start with the same 17 year calibration period (1996–2012) but diverge after this period. In the first scenario, meant to represent status quo conditions, years were randomly selected using a pseudo random number generator with a uniform distribution, such that all years had an equal probability of selection. In the second scenario, meant to represent sea-ice loss over time, a distribution function was used to bias the selection towards lower ice-index bins as the scenario progressed. Once a bin was selected, a year was chosen from that specified bin; all years within the selected bin had an equal probability of selection using a uniform random distribution. The following selection function was used to randomly select a bin:

$$\text{Bin} = \text{Truncation}[4 * R^{f(t)}] \quad (\text{D1})$$

where Bin is the pre-defined sea-ice index bins 0, 1, 2, and 3. Truncation is a function that rounds down to the nearest integer less than or equal to the value. The constant 4 represents the four ice index bins and scales the output to produce a whole number between zero and three inclusive. R is a pseudo random number with a uniform distribution such that $0 \leq R < 1$. The function $f(t)$, as defined in Eq. (D2), determines the rate at which the biasing shifts towards the lowest sea-ice index bin (bin 0). The value of $f(t)$ changes at each annual time step. The output from this function selects the bin that a year will then be randomly selected from, for each year in the 100-year time series.

Eq. (D2) was used to determine the annual exponent in Eq. (D1). The output from Eq. (D2) is a value between 1 and 20 inclusive, and changes each year of the time series.

$$f(t) = 1 + \left(19 * \left(\frac{t}{100} \right)^3 \right) \quad (\text{D2})$$

where t is a year in the 100-year time series from 1 to 100. The constant value 1, ensures that the output of Eq. (D2) is greater than or equal to 1. Without this addition Eq. (D2) would bias selection towards high sea-ice index years. The constant 19 and the power of 3 influence how quickly the selection is biased towards bin 0. Several different values for the constant and power were tested, these values were selected because effects of biasing were noticeable within the first 20 years and did not become extreme until later in the time series.

The effectiveness of our biasing function was illustrated by examining the distributions of selection probabilities at four discrete time steps in the 100-year series (Fig. D1). The resulting sea-ice time series, and corresponding sea-ice indices for both the status quo scenario and decreasing sea-ice scenario are shown in Fig. D2.

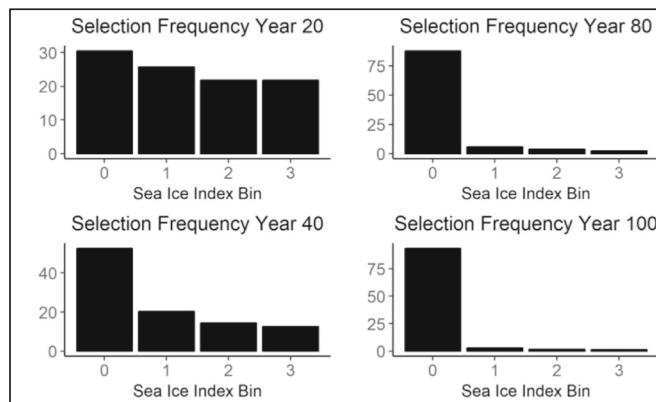


Fig. D1. Distributions of selected sea-ice index bins. At each time step, 4000 selections were performed. The bars represent the frequency that each sea-ice index bin was selected at the specified time step. The biasing function strongly favors the lowest ice-index bin by about year 40.

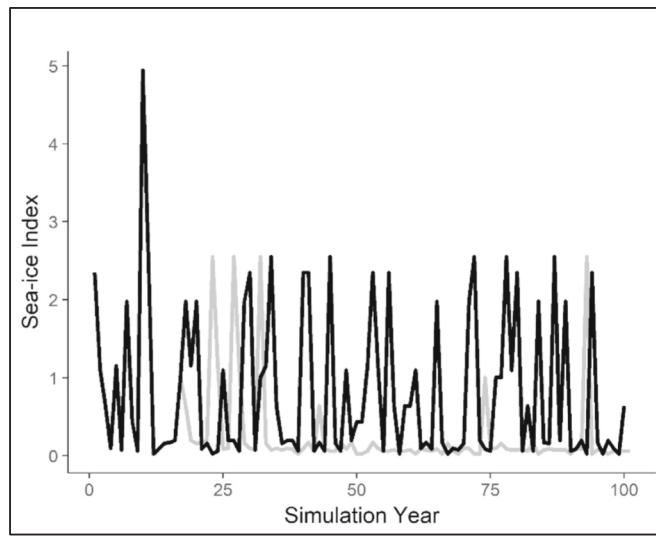


Fig. D2. Sea-ice indices for 100-year scenarios. Illustration of sea-ice indices for years selected for the status quo (black) and the decreasing ice (grey) 100-year scenarios. The scenarios use the same set of data for the first 17 years (1996–2012) and then diverge.

Once the 100-year sea-ice time series were selected, all other forcing functions in Ecosim and Ecospace were constructed from existing data, using the same years of data as were selected for sea-ice and were matched by year to complete both the status quo ice scenario and the decreasing ice scenario. Specifically, data describing open water area and chlorophyll *a* concentration, were parsed annually and sequenced in the same order as the sea-ice index data for each scenario. Similarly, sea-ice concentration and open water ASCII files were ordered to match the newly selected 100-year time series and fed into Ecospace using the external data framework (Steenbeek et al., 2013).

Appendix E. Comparison of results for Adélie Penguins under different ice conditions

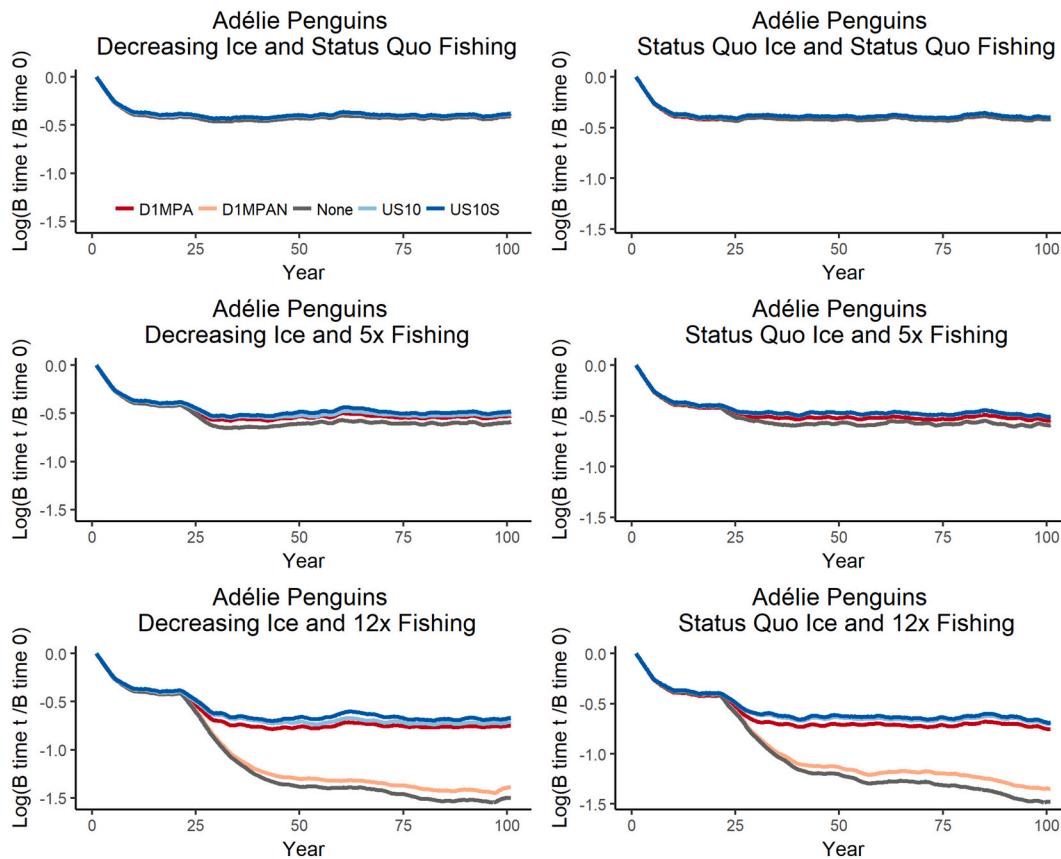


Fig. E1. Model results for Adélie penguins under varying ice conditions and fishing pressure. Line color denotes marine protected area scenario, or the absence of a marine protected area (grey line). The y-axis denotes the Log of the ratio between the biomass (B) at time t divided the biomass at time zero. Negative values indicate a biomass decline measured against the biomass at the start of the simulations.

References

- Acker, J.G., Leptoukh, G., 2007. Online analysis enhances use of NASA earth science data. *Eos, Transactions American Geophysical Union* 88, 14–17.
- Adam, P.J., 2005. Lobodon carcinophaga. Mamm. Species 1–14.
- Ashjian, C.J., Davis, C.S., Gallager, S.M., Wiebe, P.H., Lawson, G.L., 2008. Distribution of larval krill and zooplankton in association with hydrography in Marguerite Bay, Antarctic Peninsula, in austral fall and winter 2001 described using the Video Plankton Recorder. *Deep-Sea Res. II Top. Stud. Oceanogr.* 55, 455–471.
- Atkinson, A., Siegel, V., Pakhomov, E., Rothery, P., 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432, 100–103.
- Atkinson, A., Siegel, V., Pakhomov, E.A., Jessopp, M.J., Loeb, V., 2009. A re-appraisal of the total biomass and annual production of Antarctic krill. *Deep-Sea Res. I Oceanogr. Res. Pap.* 56, 727–740.
- Atkinson, A., Hill, S.L., Pakhomov, E.A., Siegel, V., Reiss, C.S., Loeb, V.J., Steinberg, D.K., Schmidt, K., Tarling, G.A., Gerrish, L., Sailley, S.F., 2019. Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. *Nat. Clim. Chang.* 9, 142–147.
- Ballerini, T., Hofmann, E.E., Ainley, D.G., Daly, K., Marrari, M., Ribic, C.A., Smith Jr., W.O., Steele, J.H., 2014. Productivity and linkages of the food web of the southern region of the western Antarctic peninsula continental shelf. *Prog. Oceanogr.* 122, 10–29.
- Bengtson, J.L., Hill, R.D., Hill, S.L., 1993. Using satellite telemetry to study the ecology and behavior of Antarctic seals. *Korean Journal of Polar Research* 4, 109–115.
- Bost, C.A., Thiebot, J.B., Pinaud, D., Cherel, Y., Trathan, P.N., 2009. Where do penguins go during the inter-breeding period? Using geolocation to track the winter dispersion of the macaroni penguin. *Biol. Lett.* 5, 473–476.
- Brooks, C.M., 2013. Competing values on the Antarctic high seas: CCAMLR and the challenge of marine-protected areas. *The Polar Journal* 3, 277–300.
- Burns, J.M., Costa, D.P., Fedak, M.A., Hindell, M.A., Bradshaw, C.J.A., Gales, N.J., McDonald, B., Trumble, S.J., Crocker, D.E., 2004. Winter habitat use and foraging behavior of crabeater seals along the Western Antarctic Peninsula. *Deep-Sea Res. II Top. Stud. Oceanogr.* 51, 2279–2303.
- Burns, J.M., Hindell, M.A., Bradshaw, C.J.A., Costa, D.P., 2008. Fine-scale habitat selection of crabeater seals as determined by diving behavior. *Deep-Sea Res. II Top. Stud. Oceanogr.* 57, 778–791.
- Stud. Oceanogr. 55, 500–514.
- Carbotte, S.M., Ryan, W.B.F., O'Hara, S., Arko, R., Goodwillie, A., Melkonian, A., Weissel, R.A., Ferrini, V.L., 2007. Antarctic Multibeam Bathymetry and Geophysical Data Synthesis: An On-line Digital Data Resource for Marine Geoscience Research in the Southern Ocean. U.S. Geological Survey Open-File Report.
- Cavalieri, D.J., Parkinson, C.L., Gloersen, P., Zwally, H.J., 1996, updated yearly. Sea Ice Concentrations from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data, Version 1 South Monthly subset, ed. NASA National Snow and Ice Data Center Distributed Active Archive Center, Boulder, Colorado USA, doi: <https://doi.org/10.5067/8GQ8LZQVLOVL> [Accessed January 16, 2017].
- CCAMLR, 2008. Report of the 27th meeting of the Commission. Available from: <https://www.ccamlr.org/en/ccamlr-xvii>.
- CCAMLR, 2011. Conservation Measure 91–04. General Framework for the Establishment of CCAMLR Marine Protected Areas. Available at: <https://www.ccamlr.org/en/measure-91-04-2011>.
- CCAMLR, 2016. Conservation measure 51–07. Interim distribution in the trigger level for the fishery for *Euphausia superba* in statistical subareas 48.1, 48.2, 48.3 and 48.4. Available at: <https://www.ccamlr.org/en/measure-51-07-2016>.
- CCAMLR, 2017, 122 pp. available at: <https://www.ccamlr.org/en/system/files/e-cc-xxxvi-0.pdf>. Report of the 36th meeting of the commission, Hobart, Tasmania.
- CCAMLR, 2018. CCAMLR Statistical Bulletin. 30. Available at: <http://www.ccamlr.org/en/data/statistical-bulletin>.
- Chapman, E.W., Hofmann, E.E., Patterson, D.L., Ribic, C.A., Fraser, W.R., 2011. Marine and terrestrial factors affecting Adelie penguin *Pygoscelis adeliae* chick growth and recruitment off the western Antarctic peninsula. *Mar. Ecol. Prog. Ser.* 436, 273–289. <https://doi.org/10.3354/meps09242>.
- Christensen, V., Walters, C.J., 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecol. Model.* 172, 109–139.
- Christensen, V., Coll, M., Steenbeek, J., Buszowski, J., Chagaris, D., Walters, C.J., 2014. Representing variable habitat quality in a spatial food web model. *Ecosystems* 17, 1397–1412.
- Constable, A.J., de la Mare, W.K., Agnew, D.J., Everson, I., Miller, D., 2000. Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). *ICES J. Mar. Sci.* 57, 778–791.

- Constable, A.J., Melbourne-Thomas, J., Corney, S.P., Arrigo, K.R., Barbraud, C., Barnes, D.K.A., Bindoff, N.L., Boyd, P.W., Brandt, A., Costa, D.P., Davidson, A.T., Ducklow, H.W., Emmerson, L., Fukuchi, M., Gutt, J., Hindell, M.A., Hofmann, E.E., Hosie, G.W., Iida, T., Jacob, S., Johnston, N.M., Kawaguchi, S., Kokubun, N., Koubari, P., Lea, M.-A., Makhalo, A., Massom, R.A., Meiners, K., Meredith, M.P., Murphy, E.J., Nicol, S., Reid, K., Richerson, K., Riddle, M.J., Rintoul, S.R., Smith, W.O., Southwell, C., Stark, J.S., Sumner, M., Swadling, K.M., Takahashi, K.T., Trathan, P.N., Welsford, D.C., Weimerskirch, H., Westwood, K.J., Wienecke, B.C., Wolf-Gladrow, D., Wright, S.W., Xavier, J.C., Ziegler, P., 2014. Climate change and Southern Ocean ecosystems I: how changes in physical habitats directly affect marine biota. *Glob. Chang. Biol.* 20, 3004–3025. <https://doi.org/10.1111/gcb.12623>.
- Cornejo-Donoso, J., Antezana, T., 2008. Preliminary trophic model of the Antarctic Peninsula Ecosystem (Sub-area CCAMLR 48.1). *Ecol. Model.* 218, 1–17.
- Costa, D.P., Huckstadt, L.A., Crocker, D.E., McDonald, B.I., Goebel, M.E., Fedak, M.A., 2010. Approaches to studying climatic change and its role on the habitat selection of Antarctic pinnipeds. *Integr. Comp. Biol.* 50, 1018–1030.
- Croxall, J.P., Trathan, P.N., Murphy, E.J., 2002. Environmental change and Antarctic seabird populations. *Science* 297, 1510–1514.
- Dahod, A., Watters, G.M., de Mutsert, K., 2019. Using sea ice to calibrate a dynamic trophic model for the Western Antarctic Peninsula region. *Plos One*.
- Davis, R.W., Fuiman, L.A., Williams, T.M., Collier, S.O., Hagey, W.P., Kanatous, S.B., Kohin, S., Horning, M., 1999. Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* 283, 993–996.
- Delegations of Argentina and Chile, 2017a. Domain 1 Marine Protected Area Preliminary Proposal Part A-1: Priority Areas for Conservation. SC-CAMLR- XXXVI/17.
- Delegations of Argentina and Chile, 2017b. Domain 1 Marine Protected Area Preliminary Proposal Part A-2: MPA Model. SC-CAMLR- XXXVI/18.
- DeWitt, H.H., Heemstra, P.C., Gon, O., 1990. Nototheniidae, In Fishes of the Southern Ocean. eds O. Gon, P.C. Heemstra, pp. 279–331. J.L.B Smith Institute of Ichthyology, Grahamstown, South Africa.
- Ducklow, H.W., Baker, K., Martinson, D.G., Quetin, L.B., Ross, R.M., Smith, R.C., Stammerjohn, S.E., Vernet, M., Fraser, W., 2007. Marine pelagic ecosystems: The West Antarctic Peninsula. *Philosophical Transactions of the Royal Society B-Biological Sciences* 362, 67–94.
- Ducklow, H.W., Fraser, W.R., Meredith, M.P., Stammerjohn, S.E., Doney, S.C., Martinson, D.G., Sailley, S.F., Schofield, O.M., Steinberg, D.K., Venables, H.J., Amsler, C.D., 2013. West Antarctic Peninsula: an ice-dependent coastal marine ecosystem in transition. *Oceanography* 26, 190–203.
- Emslie, S.D., Patterson, W.P., 2007. Abrupt recent shift in delta¹³C and delta¹⁵N values in Adelie penguin eggshell in Antarctica. *Proc. Natl. Acad. Sci. U. S. A.* 104, 11666–11669.
- Erdmann, E.S., Ribic, C.A., Patterson-Fraser, D.L., Fraser, W.R., 2011. Characterization of winter foraging locations of Adélie penguins along the Western Antarctic Peninsula, 2001–2002. *Deep-Sea Res. II Top. Stud. Oceanogr.* 58, 1710–1718.
- Erfran, A., Pitcher, T.J., 2005. An ecosystem simulation of the Antarctic Peninsula, In Fisheries Centre Research Reports: Modeling Antarctic Marine Ecosystems. eds M.L. D. Palomares, P. Pruvost, T.J. Pitcher, D. Pauly, pp. 5–20. University of British Columbia, Vancouver, BC Canada.
- Fahrbach, E., Rohardt, G., Krause, G., 1992. The Antarctic coastal current in the south-eastern Weddell Sea. *Polar Biol.* 12, 171–182.
- Fisher, E.C., Kaufmann, R.S., Smith, K.L., 2004. Variability of epipelagic macrozooplankton/microneuston community structure in the NW Weddell Sea, Antarctica (1995–1996). *Mar. Biol.* 144, 345–360.
- Forcada, J., Trathan, P.N., Reid, K., Murphy, E.J., Croxall, J.P., 2006. Contrasting population changes in sympatric penguin species in association with climate warming. *Glob. Chang. Biol.* 12, 411–423.
- Forcada, J., Trathan, P.N., Boveng, P.L., Boyd, I.L., Burns, J.M., Costa, D.P., Fedak, M., Rogers, T.L., Southwell, C.J., 2012. Responses of Antarctic pack-ice seals to environmental change and increasing krill fishing. *Biol. Conserv.* 149, 40–50.
- Fraser, W.R., Trivelpiece, W.Z., Ainley, D.G., Trivelpiece, S.G., 1992. Increases in Antarctic penguin populations - reduced competition with whales or a loss of sea ice due to environmental warming. *Polar Biol.* 11, 525–531.
- Frazer, T.K., Quetin, L.B., Ross, R.M., 2002. Abundance, sizes and developmental stages of larval krill, *Euphausia superba*, during winter in ice-covered seas west of the Antarctic Peninsula. *J. Plankton Res.* 24, 1067–1077.
- Friedlaender, A.S., Johnston, D.W., Fraser, W.R., Burns, J., Patrick N, H., Costa, D.P., 2011. Ecological niche modeling of sympatric krill predators around Marguerite Bay, Western Antarctic Peninsula. *Deep-Sea Res. II Top. Stud. Oceanogr.* 58, 1729–1740.
- Gaines, S.D., White, C., Carr, M.H., Palumbi, S.R., 2010. Designing marine reserve networks for both conservation and fisheries management. *Proc. Natl. Acad. Sci. U. S. A.* 107, 18286–18293.
- Gell, F.R., Roberts, C.M., 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol. Evol.* 18, 448–455.
- Goebel, M.E., Reiss, C., 2014. Squeezed from both ends: decline in Antarctic fur seals in the South Shetland Islands driven by both top-down and bottom-up processes. WG-EMM-14-39; data available at. <https://data.nodc.noaa.gov/cgi-bin/iso?id=gov.noaa.nodc:0186008>.
- Gorman, K.B., Erdmann, E.S., Pickering, B.C., Horne, P.J., Blum, J.R., Lucas, H.M., Patterson-Fraser, D.L., Fraser, W.R., 2010. A new high-latitude record for the macaroni penguin (*Eudyptes chrysophthalmus*) at Avian Island, Antarctica. *Polar Biol.* 33, 1155–1158.
- Green, J.A., Boyd, I.L., Woakes, A.J., Warren, N.L., Butler, P.J., 2005. Behavioural flexibility during year-round foraging in macaroni penguins. *Mar. Ecol. Prog. Ser.* 296, 183–196.
- Gutt, J., Barnes, D.K.A., Lockhart, S.J., Van de Putte, A.P., 2013. Antarctic macrobenthic communities: a compilation of circumpolar information. *Nature Conservation* 4, 1–13.
- Hill, S.L., Reid, K., Thorpe, S.E., Hinke, J., Watters, G.M., 2007. A compilation of parameters for ecosystem dynamics models of the Scotia Sea-Antarctic Peninsula region. *CCAMLR Science* 14, 1–25.
- Hill, S.L., Phillips, T., Atkinson, A., 2013. Potential climate change effects on the habitat of Antarctic krill in the Weddell quadrant of the Southern Ocean. *PLoS One* 8, e72246.
- Hinke, J.T., Salwicka, K., Trivelpiece, S.G., Watters, G.M., Trivelpiece, W.Z., 2007. Divergent responses of Pygoscelis penguins reveal a common environmental driver. *Oecologia* 153, 845–855.
- Hinke, J., Trivelpiece, S., Trivelpiece, W., 2014. Adélie penguin (*Pygoscelis adeliae*) survival rates and their relationship to environmental indices in the South Shetland Islands, Antarctica. *Polar Biol.* 37, 1797–1809.
- Hinke, J.T., Polito, M.J., Goebel, M.E., Jarvis, S., Reiss, C.S., Thorrold, S.R., Trivelpiece, W.Z., Watters, G.M., 2015. Spatial and isotopic niche partitioning during winter in chinstrap and Adélie penguins from the South Shetland Islands. *Ecosphere* 6, 1–32.
- Hinke, J.T., Cossio, A.M., Goebel, M.E., Reiss, C.S., Trivelpiece, W.Z., Watters, G.M., 2017. Identifying risk: concurrent overlap of the Antarctic krill fishery with krill-dependent predators in the Scotia Sea. *PLoS One* 12, e0170132.
- Horsburgh, J.M., Morrice, M., Lea, M.-a., Hindell, M.A., 2008. Determining feeding events and prey encounter rates in a southern elephant seal: a method using swim speed and stomach temperature. *Marine Mammal Science* 24, 207–217.
- Hückstädt, L.A., Koch, P.L., McDonald, B.I., Goebel, M.E., Crocker, D.E., Costa, D.P., 2012. Stable isotope analyses reveal individual variability in the trophic ecology of a top marine predator, the southern elephant seal. *Oecologia* 169, 395–406.
- Huntley, M., Brinton, E., 1991. Mesoscale variation in growth and early development of *Euphausia superba Dana* in the western Bransfield Strait region. *Deep Sea Research Part A Oceanographic Research Papers* 38, 1213–1240.
- IPCC, 2013. Summary for policy makers, In Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change eds T.F. Stocker, D. Qin, G.K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, P.M. Midgley, p. 28 pp., Cambridge, United Kingdom and New York, USA.
- Iwami, T., Kock, K.H., 1990. Channichthyidae, In Fishes of the Southern Ocean. eds O. Gon, P.C. Heemstra, pp. 381–399. J.L.B Smith Institute of Ichthyology, Grahamstown, South Africa.
- Jenouvrier, S., Barbraud, C., Cazelles, B., Weimerskirch, H., 2005. Modelling population dynamics of seabirds: importance of the effects of climate fluctuations on breeding proportions. *Oikos* 108, 511–522.
- Jones, C.D., Parker, S.J., 2016. Vignette 4: local sea-ice dynamics is linked to krill-fishing operations, In Background Information to Support Developmental Feedback Management Strategy for the Krill Fishery in Subarea 48.1. ed. Antarctic Ecosystem Research Division Southwest Fisheries Science Center and NOAA Fisheries, pp. 34–40 WG-EMM-16/45.
- Kemp, S., Bennett, A.G., 1932. On the distribution and movements of whales on the South Georgia and South Shetland whaling grounds. *Discovery Reports*, Cambridge University Press London 6.
- Kirkwood, R., Robertson, G., 1997. The foraging ecology of female emperor penguins in winter. *Ecol. Monogr.* 67, 155–176.
- Klein, E.S., Watters, G.M., 2020. What's the catch? Profiling the risks and costs associated with marine protected areas and displaced fishing in the Scotia Sea. *PLoS One* (in press).
- Klein, E.S., Hill, S.L., Hinke, J.T., Phillips, T., Watters, G.M., 2018. Impacts of rising sea temperature on krill increase risks for predators in the Scotia Sea. *PLoS One* 13, e0191011. <https://doi.org/10.1371/journal.pone.0191011>.
- Kock, K.-H., Jones, C.D., 2005. Fish stocks in the southern Scotia Arc region—a review and prospects for future research. *Rev. Fish. Sci.* 13, 75–108.
- Link, J.S., Ihde, T.F., Harvey, C.J., Gaichas, S.K., Field, J.C., Brodziak, J.K.T., Townsend, H.M., Peterman, R.M., 2012. Dealing with uncertainty in ecosystem models: the paradox of use for living marine resource management. *Prog. Oceanogr.* 102, 102–114.
- Lockhart, S.J., Jones, C.D., 2008. Biogeographic patterns of benthic invertebrate megafauna on shelf areas with the Southern Ocean Atlantic sector. *CCAMLR Science* 15, 167–192.
- Lynch, H.J., Naveen, R., Trathan, P.N., Fagan, W.F., 2012. Spatially integrated assessment reveals widespread changes in penguin populations on the Antarctic Peninsula. *Ecology* 93, 1367–1377.
- Martell, S.J.D., Essington, T.E., Lessard, B., Kitchell, J.F., Walters, C.J., Boggs, C.H., 2005. Interactions of productivity, predation risk, and fishing effort in the efficacy of marine protected areas for the central Pacific. *Can. J. Fish. Aquat. Sci.* 62, 1320–1336.
- Martinson, D.G., Stammerjohn, S.E., Iannuzzi, R.A., Smith, R.C., Vernet, M., 2008. Western Antarctic Peninsula physical oceanography and spatio-temporal variability. *Deep-Sea Research Part II-Topical Studies in Oceanography* 55, 1964–1987.
- Meade, J., Ciaglia, M., Slip, D., Negrete, J., Márquez, M., Mennucc, i.J., Rogers, T., 2015. Spatial patterns in activity of leopard seals *Hydrurga leptonyx* in relation to sea ice. *Mar. Ecol. Prog. Ser.* 521, 265–275.
- Melbourne-Thomas, J., Corney, S.P., Trebilco, R., Meiners, K.M., Stevens, R.P., Kawaguchi, S., Sumner, M.D., Constable, A.J., 2016. Under ice habitats for Antarctic krill larvae: could less mean more under climate warming? *Geophys. Res. Lett.* 43, 10,322–310,327.
- Motani, R., 2002. Scaling effects in caudal fin propulsion and the speed of ichthyosaurs. *Nature* 415, 309–312.
- Naveen, R., Lynch, H.J., 2011. Antarctic Peninsula Compendium, 3rd edition.
- Nicol, S., Foster, J., Kawaguchi, S., 2012. The fishery for Antarctic krill - recent developments. *Fish Fish.* 13, 30–40.

- Nordøy, E.S., Folkow, L., Blix, A.S., 1995. Distribution and diving behaviour of crabeater seals (*Lobodon carcinophagus*) off Queen Maud Land. *Polar Biol.* 15, 261–268.
- O'Dor, R., 2002. Telemetered cephalopod energetics: swimming, soaring, and blimping. *Integr. Comp. Biol.* 42, 1065–1070.
- Pakhomov, E.A., Atkinson, A., Meyer, B., Oettl, B., Bathmann, U., 2004. Daily rations and growth of larval krill *Euphausia superba* in the Eastern Bellingshausen Sea during austral autumn. *Deep-Sea Res. II Top. Stud. Oceanogr.* 51, 2185–2198.
- Reiss, C.S., Cossio, A., Santora, J.A., Dietrich, K.S., Murray, A., Mitchell, B.G., Walsh, J., Weiss, E.L., Gimpel, C., Jones, C.D., Watters, G.M., 2017. Overwinter habitat selection by Antarctic krill under varying sea-ice conditions: implications for top predators and fishery management. *Mar. Ecol. Prog. Ser.* 568, 1–16.
- Richerson, K., Watters, G.M., Santora, J.A., Schroeder, I.D., Mangel, M., 2015. More than passive drifters: a stochastic dynamic model for the movement of Antarctic krill. *Mar. Ecol. Prog. Ser.* 529, 35–48.
- Roberts, C.M., O'Leary, B.C., McCauley, D.J., Cury, P.M., Duarte, C.M., Lubchenco, J., Pauly, D., Sáenz-Arroyo, A., Sumaila, U.R., Wilson, R.W., Worm, B., Castilla, J.C., 2017. Marine reserves can mitigate and promote adaptation to climate change. *PNAS* 114, 6167–6175. <https://doi.org/10.1073/pnas.1701262114>.
- Rogers, T.L., Hogg, C.J., Irvine, A., 2005. Spatial movement of adult leopard seals (*Hydrurga leptonyx*) in Prydz Bay, Eastern Antarctica. *Polar Biol.* 28, 456–463.
- Sambilay, V.J., 1990. Interrelationships between swimming speed, caudal fin aspect ratio and body length of fishes. *Fishbyte* 8, 16–20.
- SC-CAMLR, 2005. Report of the twenty fourth meeting of the Scientific Committee. Available at: <https://www.ccamlr.org/en/sc-camlr-xxiv>.
- Scheffers, B.R., Meester, L.D., Bridge, T.C.L., Hoffmann, A.A., Pandolfi, J.M., Corlett, R.T., Butchart, S.H.M., Pearce-Kelly, P., Kovacs, K.M., Dodgeon, D., Pacifici, M., Rondinini, C., Foden, W.B., Martin, T.G., Mora, C., Bickford, D., Watson, J.E.M., 2016. The broad footprint of climate change from genes to biomes to people. *Science* 354. <https://doi.org/10.1126/science.aaf7671>.
- Second WS-MPA Domain 1, 2015. Report of the Second International Workshop for Identifying Marine Protected Areas (MPAs) in Domain 1 of CCAMLR (Palacio San Martin, Buenos Aires, Argentina), WG-EMM-15-42.
- Siegel, V., Reiss, C.S., Dietrich, K.S., Haraldsson, M., Rohardt, G., 2013. Distribution and abundance of Antarctic krill (*Euphausia superba*) along the Antarctic Peninsula. *Deep-Sea Res. I Oceanogr. Res. Pap.* 77, 63–74.
- Stammerjohn, S.E., Martinson, D.G., Smith, R.C., Iannuzzi, R.A., 2008. Sea ice in the western Antarctic Peninsula region: Spatio-temporal variability from ecological and climate change perspectives. *Deep Sea Research Part II: Topical Studies in Oceanography*, Palmer, Antarctica Long Term Ecological Research 55, 2041–2058. <https://doi.org/10.1016/j.dsr2.2008.04.026>.
- Steenbeek, J., Coll, M., Gurney, L., Mélin, F., Hoepffner, N., Buszowski, J., Christensen, V., 2013. Bridging the gap between ecosystem modeling tools and geographic information systems: driving a food web model with external spatial-temporal data. *Ecol. Model.* 263, 139–151.
- Suprenand, P.M., Ainsworth, C.H., 2017. Trophodynamic effects of climate change-induced alterations to primary production along the western Antarctic Peninsula. *Mar. Ecol. Prog. Ser.* 569, 37–54.
- Tarling, G.A., Thorpe, S.E., 2014. Instantaneous movement of krill swarms in the Antarctic Circumpolar Current. *Limnol. Oceanogr.* 59, 872–886.
- Taylor, B.L., Baird, R., Barlow, J., Dawson, S.M., Ford, J., Mead, J.G., Notarbartolo di Sciara, G., Wade, P., Pitman, R.I., 2008. *Physeter macrocephalus*. The IUCN Red List of Threatened Species 2008 e.T41755A10554884.
- Trivelpiece, W.Z., Trivelpiece, S.G., Volkman, N.J., 1987. Ecological segregation of Adelie, gentoo, and chinstrap penguins at King George Island. *Antarctica Ecology* 68, 351–361.
- Trivelpiece, W.Z., Hinke, J.T., Miller, A.K., Reiss, C.S., Trivelpiece, S.G., Watters, G.M., 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proc. Natl. Acad. Sci.* 108, 7625–7628.
- Vernet, M., Martinson, D., Iannuzzi, R., Stammerjohn, S., Kozlowski, W., Sines, K., Smith, R., Garibotti, I., 2008. Primary production within the sea-ice zone west of the Antarctic Peninsula: I—sea ice, summer mixed layer, and irradiance. *Deep Sea Research Part II: Topical Studies in Oceanography* 55, 2068–2085.
- Walters, C., Pauly, D., Christensen, V., 1999. Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* 2, 539–554.
- Watanabe, Y.Y., Sato, K., Watanuki, Y., Takahashi, A., Mitani, Y., Amano, M., Aoki, K., Narazaki, T., Iwata, T., Minamikawa, S., Miyazaki, N., 2011. Scaling of swim speed in breath-hold divers. *J. Anim. Ecol.* 80, 57–68.
- Watters, G., 2015. Report of a Domestic Workshop to Identify U.S. Stakeholders' Objectives and Protection Priorities for One or More Marine Protected Areas in Planning Domain 1. WG-EMM 15/34.
- Watters, G.M., Hinke, J.T., Reiss, C.S., 2020. Long-term observations from Antarctica demonstrate that mismatched scales of fisheries management and predator-prey interaction lead to erroneous conclusions about precaution. *Sci. Rep.* 10, 2314. <https://doi.org/10.1038/s41598-020-59223-9>.
- Whitehead, H., 2003. *Sperm Whales: Social Evolution in the Ocean*. University of Chicago Press, Chicago, IL, USA.
- Wienecke, B., Robertson, G., 1997. Foraging space of emperor penguins *Aptenodytes forsteri* in Antarctic shelf waters in winter. *Mar. Ecol. Prog. Ser.* 159, 249–263.
- Williams, R., Noren, D.P., 2009. Swimming speed, respiration rate, and estimated cost of transport in adult killer whales. *Marine Mammal Science* 25, 327–350.
- Zerbini, A.N., Adams, G., Best, J., Clapham, P.J., Jackson, J.A., Punt, A.E., 2019. Assessing the recovery of an Antarctic predator from historical exploitation. *Royal Society Open Science*. 6:190368. doi:10.1098/rsos.190368.