

CONSERVING BIODIVERSITY IN THE WESTERN ANTARCTIC PENINSULA
REGION: MARINE PROTECTED AREA DESIGN AND POLICY IMPLICATIONS

by

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DEDICATION

For my mom, who would have loved to finally see me walk across a stage

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LIST OF ABBREVIATIONS

Antarctic Marine Living Resources	AMLRL
Antarctic Peninsula Pelagic Area	APPA
Antarctic Peninsula West.....	APW
Antarctic Treaty Consultative Meeting.....	ATCM
Antarctic Treaty System	ATS
Assimilation Efficiency	AE
The CCAMLR Ecosystem Monitoring Programme	CEMP
Coefficient of Variation	CV
Commission for the Conservation of Antarctic Marine Living Resources.....	CCAMLR
Conservation of Antarctic Marine Living Resources	CAMLR
Conservation Measure	CM
Consumption to Biomass Ratio	Q/B
Ecopath with Ecosim	EwE
Ecotrophic Efficiency	EE
La Jolla Workshop Top 5%	LJ5
La Jolla Workshop Top 10%	LJ10
Long Term Ecological Research.....	LTER
Marine Protected Area	MPA
Monte Carlo	MC
National Oceanographic and Atmospheric Administration.....	NOAA
Production Efficiency	PE
Production to Biomass Ratio	P/B
Production to Consumption Ratio.....	P/Q
Scientific Committee of the Commission for the Conservation of Antarctic Marine Living Resources	SC-CAMLR
Small Scale Management Unit	SSMU
Sum of Squares Difference	SS
Systematic Conservation Planning	SCP
United Kingdom.....	UK
United States	U.S.
Western Antarctic Peninsula.....	WAP

ABSTRACT

CONSERVING BIODIVERSITY IN THE WESTERN ANTARCTIC PENINSULA REGION: MARINE PROTECTED AREA DESIGN AND POLICY IMPLICATIONS

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Well-designed marine protected areas (MPAs) help preserve biodiversity and contribute to the management of sustainable fisheries. MPAs may be particularly important in environments where sea-ice loss is rapidly increasing areas available to fisheries. The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) has recognized that establishing MPAs could help achieve its conservation and fisheries management goals. The CCAMLR has agreed on objectives to be met by future MPAs. Two of these objectives relate to preserving ecosystem processes and functions. Antarctic MPA design processes to date have relied on static maps of biodiversity values and human use patterns to inform boundary selection. Such processes assume spatial stability of the ecosystem functions and processes that created observed patterns of distribution and abundance. This work seeks to supplement the CCAMLR MPA planning process by using dynamic food web modeling to inform MPA boundary

selection. Ecopath with Ecosim is a multi-tiered dynamic food web modeling software package. It was used to develop a mass balanced food web model (Ecopath), time dynamic simulations of the food web (Ecosim), and spatially and temporally dynamic simulations (Ecospace) for the Western Antarctic Peninsula (WAP) region. Ecospace simulations were used to evaluate the impact of four MPA boundary scenarios on biomass accumulation patterns. These analyses effectively evaluated if the proposed boundaries would protect ecosystem processes that contribute to biomass accumulation. The Ecopath model was designed to include all currently monitored species as single species groups to facilitate MPA planning. The Ecosim model was successfully calibrated for the years 1996-2012 using time dynamic simulations. When sea-ice temporal dynamics were included as forcing functions, the model recreated trends in abundance for key monitored species. Ecospace simulations included spatial aspects of the sea-ice regime and adequately represented spatial trends in biomass accumulation for the years 1996-2012. 100-year scenarios were developed that examined the impact of sea-ice conditions, fishing levels, and MPA boundary configurations. Scenario evaluation illustrated the importance of fishing level in influencing spatial patterns of biomass accumulation. While MPA scenario evaluation highlighted that to be effective in the WAP an MPA must be very large, be in place for an extended period, and could consider including southern regions that may have increased importance as sea-ice loss progresses. The aim of this research is to use insights gained from spatio-temporal dynamic food web modeling to contribute to the discussion on which areas to prioritize for protection in the Western Antarctic Peninsula region.

CHAPTER ONE: GENERAL INTRODUCTION

Antarctica and its marine environments are unique both ecologically and politically. The marine ecosystems throughout the Antarctic are recognized as experiencing very few anthropogenic impacts when compared to other coastal regions (Halpern et al. 2008). This implies that much of the original Antarctic marine biodiversity likely is still present. Accordingly, there is interest in creating Antarctic marine protected areas (MPAs) before significant biodiversity losses occur (Brooks 2013). Antarctica is collectively governed by all nations that have acceded to the Antarctic Treaty (Antarctic Treaty 1959). An instrument of the Antarctic Treaty System, the Convention on the Conservation of Antarctic Marine Living Resources (CAMLRL), governs Antarctic marine environments and allows for the closure of areas to fishing to further conservation efforts (Convention on the Conservation of Antarctic Marine Living Resources 1980, Article IX, paragraph 2 g). Under the CAMLR Convention, decisions are made by consensus (Convention on the Conservation of Antarctic Marine Living Resources 1980, Constable et al. 2000) and any agreement to create Antarctic MPAs would need the support of all Members to the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). In 2005, the Scientific Committee for the Conservation of Antarctic Marine Living Resources (SC-CAMLRL) prioritized creating a representative system of marine protected areas throughout Antarctica (SC-CAMLRL 2005, paragraphs 3.54 i, iv-b and iv-

c) thus officially starting the process of creating Antarctic MPAs. In 2011 SC- CCAMLR hosted an MPA workshop to help advance efforts to designate new Antarctic MPAs, and identified Planning Domain 1 (the Western Antarctic Peninsula region and Scotia Sea) as an area ripe for MPA planning (CCAMLR 2011b). There is an existing MPA in the Scotia Sea (Figure 1), near the South Orkney Islands (CCAMLR 2009), therefore efforts in Planning Domain 1 could be more productively focused on the Western Antarctic Peninsula (WAP) region.

The Dynamic Western Antarctic Peninsula

The WAP region is the northernmost and most readily accessible Antarctic region. Due to the easy access and abundance of wildlife, human activities are concentrated there. Much of the commercial fishing effort in the Antarctic is focused in the productive waters of the WAP region (CCAMLR 2017). There are approximately 40 National Antarctic Program stations or camps in the WAP, which represents approximately 40% of all Antarctic stations (Council of Managers of National Antarctic Programs 2017) and as a result there is a concentration of scientific activities in the region. The WAP is one of the better studied Antarctic regions and much is known about climate patterns, population dynamics of top predators, population dynamics of krill, and krill fisheries activities. The WAP is contained within fisheries Statistical Subarea 48.1 and is the central region of Planning Domain 1 (Figure 1).

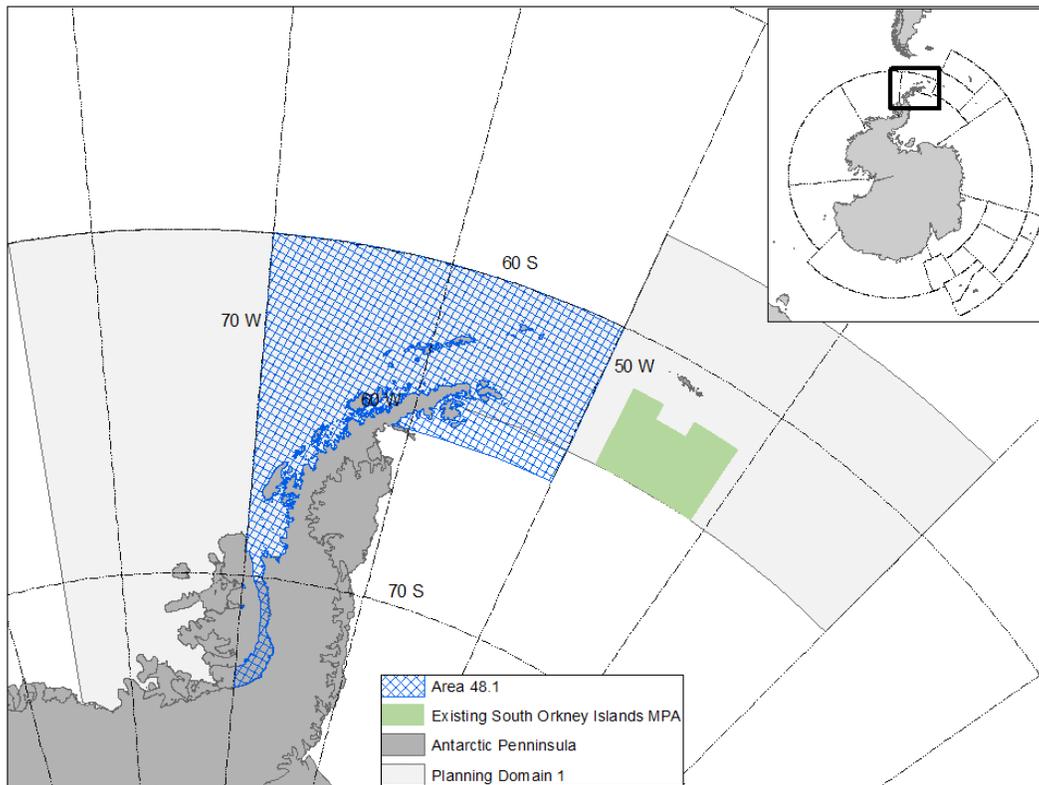


Figure 1. Map of the Western Antarctic Peninsula region.

There is a long history of meteorological observations in the WAP region dating back to the establishment of the first Antarctic stations. The longest continuous meteorological record is from a British station in the South Orkney Islands which began in 1900 (Vaughan et al. 2003). Records from across the Antarctic Peninsula region indicate a warming trend in air temperature (Ducklow et al. 2007, Trivelpiece et al. 2011, Fretwell et al. 2012, Ducklow et al. 2013). The warming is most noticeable in winter; the average winter air temperature has increased between 5-7 °C since the 1960s and is the fastest known regional warming in the world (Ducklow et al. 2007, Trivelpiece et al. 2011, Fretwell et al. 2012, Ducklow et al. 2013). The warming has resulted in an increase

in the warm summer period at a rate of 0.5+/- 0.3 days per year (Vaughan et al. 2003). Coincident with the air temperature warming there has been a marked change in precipitation patterns. Winter snowfall has increased throughout the Peninsula region (Vaughan et al. 2003) and there is greater snow accumulation (Thompson et al. 1994, Vaughan et al. 2003, Ducklow et al. 2007). It is likely that these patterns are driven by the greater number of storms coming ashore (Vaughan et al. 2003).

Warming conditions have also significantly impacted the sea-ice regime. The “permanent” ice shelves that rest over the sea have been in retreat for the past 20 years and winter sea-ice concentration and extent are currently decreasing (Ducklow et al. 2007, Stammerjohn et al. 2011, Ducklow et al. 2013). Sea-ice is forming later in the season and retreating earlier (Vaughan et al. 2003, Ducklow et al. 2007, Stammerjohn et al. 2011, Ducklow et al. 2013). Throughout the WAP the winter ice season has decreased by one to two days per year on average, with some areas experiencing a decrease of five days per year (Vaughan et al. 2003). In total, the length of the sea-ice season has shrunk, on average, approximately 92 days from 1979-80 to 2012-13 (Ducklow et al. 2013).

Temperature, precipitation patterns, and sea-ice dynamics strongly influence biological communities in the Antarctic Peninsula region (Vaughan et al. 2003, Trivelpiece et al. 2011). Every level of the food web from microbes to apex predators is influenced in some way by the sea-ice regime (Ducklow et al. 2007, Ducklow et al. 2013)

Krill

Marine ecosystems in the WAP are believed to be Antarctic krill (*Euphausia superba*) centric (Constable et al. 2000). Three broad trophic levels are typically

recognized: primary producers, krill, and krill predators (Constable et al. 2000). Krill are an essential prey source for a wide range of predators including penguins, seals, whales, fish, and cephalopods (Mori and Butterworth 2006). Krill are also the target of the largest fishery (by tonnage) in the Antarctic (Nicol et al. 2012, CCAMLR 2017). Considerable effort has been expended to understand krill ecology and document krill population trends. This is in part a reaction to the severe depletion of finfish stocks in the region that occurred before Antarctic fisheries were actively managed and reflects an international desire to avoid that same fate for krill stocks (McElroy 1984, Miller 1991).

Antarctic krill are one of the best studied pelagic organisms (Mori and Butterworth 2006, Nicol 2006). Krill concentrate on the continental shelf break and near small islands, a habitat type that is abundant in the WAP (Atkinson et al. 2004, Nicol 2006, Atkinson et al. 2009). Within the WAP, krill distribution patterns are strongly correlated with sea-ice extent; the ice provides habitat for krill and krill's algal and microbial food (Nicol 2006). Krill are patchily distributed and krill abundance can be highly variable across both time and space (Santora et al. 2009). Much of this unevenness in distribution is caused by krill's proclivity to form large swarms. Swarm size is highly variable, but swarms can extend hundreds of kilometers and contain billions of individuals (Santora et al. 2009). The enormous size of the swarms and krill's high metabolic requirements combine to make krill one of the most important macro herbivores in Antarctic waters (Nicol 2006). Krill abundance in the WAP has been declining in recent years (Atkinson et al. 2004, Atkinson et al. 2009), decreases in krill

availability may be impacting some krill predators (Trivelpiece et al. 2011, Hinke et al. 2017)

Krill Predators

Many Antarctic biological monitoring studies focus on krill predators. The CAMLR Convention and its governing body, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) require that an ecosystem approach is used to manage the krill fishery (Constable et al. 2000). To help meet this requirement CAMLR Members established an ecosystem monitoring program aimed at understanding fisheries impact on krill associated and dependent species. This program is known as the CCAMLR Ecosystem Monitoring Programme (CEMP) (Agnew 1997). CEMP is a voluntary program that has high participation from the Members (de la Mare and Constable 2000). Through CEMP and other national initiatives, population trends for penguins, seals and whales have been studied for many years. In its online database, the CCAMLR lists nine active CEMP sites in the WAP (<http://gis.CCAMLR.org/home>). Work from the CEMP monitoring has indicated that some krill predators are in decline and that there is significant overlap and competition with fisheries (Hinke et al. 2017). Management of the fishery into the future would benefit from considering such overlap and seeking to limit direct competition between central place foragers and the fishery.

Systematic Conservation Planning

The establishment of a CCAMLR MPA, is fundamentally a decision regarding which areas will experience reduced harvesting pressure. To be in accordance with the CAMLR Convention and subsequent measures adopted by the CCAMLR, such decisions

must be based upon the best available science and seek to meet several objectives including: protect representative examples of marine ecosystems, protect key ecosystem processes, establish scientific reference areas for monitoring the effects of harvesting, protect areas vulnerable to human impacts, protect features critical to ecosystem function, and protect areas to maintain resilience (CCAMLR 2011a). Systematic Conservation Planning (SCP) is a stepwise process for identifying priority areas to bring under protection (Margules and Pressey 2000, Gaston et al. 2002, Kukkala and Moilanen 2013). The aim of SCP is to protect the greatest amount of biodiversity while minimizing the negative impact on dependent human communities (Pressey et al. 1993, Margules and Pressey 2000, Margules et al. 2002). SCP is therefore likely to be a useful and politically palatable tool to investigate MPA design for the WAP.

Systematic conservation planning occurs in several stages, though the number of stages has varied since the first SCP model was introduced (reviewed in Kukkala and Moilanen 2013). SCP typically begins with identifying the planning region and compiling existing biodiversity and human-use data. These data are then used to determine conservation goals (Gaston et al. 2002). The next several stages involve assessing existing conservation areas, selecting new conservation areas, and implementing the new protections (Gaston et al. 2002). These actions can be implemented in a variety of stages (Kukkala and Moilanen 2013) and require diverse stakeholder engagement (Pressey et al. 1996).

Systematic conservation planning has been used effectively all over the world to establish terrestrial (case studies in the USA and Argentina reviewed in Didier et al.

2009) and marine (synthesis: Leslie 2005, Belgium: Douvere et al. 2007, Australia: Klein et al. 2009, Canada: Ban et al. 2013) reserves. SCP was used to design and implement Southern Ocean marine reserves at Prince Edward Island (Lombard et al. 2007), South Georgia (Collins et al. 2012), South Orkney Islands Southern Shelf (Delegation of the United Kingdom 2010) and the Ross Sea Region (Delegation of New Zealand et al. 2017). Properly designed MPAs protect a significant section of the ecosystem and can aid in the recovery of fisheries (Murawski et al. 2000, Roberts et al. 2001, Pauly et al. 2002). Marine reserves can export animals from their healthy growing populations inside the protected area into adjacent waters open to fishing (Roberts et al. 2001) and can thus serve as a fisheries management tool to help rebuild fisheries.

A sound SCP process would identify conservation goals early in the planning process and then choose planning tools that would best elucidate ways to meet those goals. The CCAMLR has endorsed the support of the planning tool Marxan, while noting that other tools could be effectively used (CCAMLR 2011b, WG-EMM 2012). Marxan is currently being used in the official MPA planning process for Planning Domain 1 (Second WS-MPA Domain 1 2015), and the process is relying heavily on static maps to design a new protected area for this very dynamic region. Often, an underlying assumption with using static maps to design protected areas is that the ecosystem processes and functions that lead to areas of biodiversity conservation are spatially stable. This may not be a valid assumption in a region that is changing as rapidly as the WAP.

The software package Ecopath with Ecosim (EwE), is commonly used to model food webs and temporal dynamics of ecosystems (Christensen and Walters 2004). The

spatial module of EwE, Ecospace, can evaluate how potential MPA boundaries could interact with dynamic trophic interactions and influence spatial and temporal patterns of biomass accumulation (Christensen and Walters 2004). Use of Ecospace to evaluate impacts on biomass accumulation patterns of potential MPA boundaries could complement the on-going the CCAMLR Marxan process to identify MPA boundaries (Second WS-MPA Domain 1 2015).

Dissertation Overview

The research presented here develops a spatially and temporally dynamic food web model in EwE, and then uses the model to evaluate four MPA boundary scenarios. The aim is that these simulations will be of interest to the Antarctic community as it continues to discuss MPA designation in the WAP.

In Chapter Two I discuss development of the mass balanced food web model (Ecopath) and time dynamic simulations (Ecosim) to ensure that the model will be useful to explore MPA design questions. The role of sea-ice in influencing trophic interactions and temporal patterns of biomass accumulation is explored. With the incorporation of sea-ice forcing, the model recreates trends of abundance for the years 1996-2012.

In Chapter Three I develop spatially and temporally dynamic simulations in Ecospace. After the simulations adequately recreated spatio-temporal patterns for the years 1996- 2012, I evaluate 100-year scenarios that explore the impacts of decreasing sea-ice and increasing fishing pressure. These 100-year scenarios serve as the baseline that MPA performance are judged against.

In Chapter Four I evaluated four MPA boundary scenarios and examine their impact on biomass accumulation patterns. The simulations explore under which conditions the potential MPAs have the greatest impact, and how long it takes for that impact to be realized. I also discuss the policy implications of the results of the MPA scenario simulations.

Chapter Five comprises the overarching conclusions for the entirety of work presented. It highlights how results of MPA scenario evaluation could be used to inform the CCAMLR MPA process.

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CHAPTER TWO: DYNAMIC TROPHIC MODEL FOR THE WESTERN ANTARCTIC PENINSULA REGION

Introduction

The Western Antarctic Peninsula region (WAP) is a data rich and dynamic region (Ducklow et al. 2007, Ducklow et al. 2013). Research and commercial fishery efforts are concentrated in the part of the WAP known as Statistical Subarea 48.1 which encompasses the western and northern Antarctic Peninsula. As a result, much is known about the ecosystems and environmental patterns in this region.

The marine food webs in the WAP are often described as krill-centric (Constable et al. 2000, Everson 2002, Hill et al. 2012, Ballerini et al. 2014). Diet studies of numerous predators in the region indicate that krill is a very important prey species for a wide variety of predators (Barrera-Oro 2002, Casaux et al. 2003, Lynnes et al. 2004, Casaux et al. 2006, Casaux et al. 2009a, Hückstädt et al. 2012a). The large biomass of krill indicates that it is a significant, if not the most significant, phytoplankton grazer in the region (Nicol 2006, Santora et al. 2009, Whitehouse et al. 2009, Hill et al. 2012). Krill are also the target of the largest (by tonnage) Antarctic fishery, with the majority of Antarctic krill landed in Statistical Subarea 48.1 (Nicol et al. 2012, CCAMLR 2017). Krill are patchily distributed, and krill abundance can be highly variable (Nicol 2006, Reiss et al. 2008, Santora et al. 2009, Reiss et al. 2017). This implies that the role of krill in the food web can vary both spatially and temporally.

The WAP is one of the most rapidly warming areas on the planet (Vaughan et al. 2003, Ducklow et al. 2007, Steig et al. 2009, Ducklow et al. 2013) with an average temperature increase of approximately 5-6° C since 1960 (Vaughan et al. 2003, Steig et al. 2009). Long-term datasets describing the sea-ice regime illustrate significant changes in response to this prolonged warming and increasing number of days where the air temperature exceeds freezing (Vaughan et al. 2003). “Permanent” ice shelves that rest over the sea have been in retreat for the past 20 years and winter sea-ice concentration and extent are both currently decreasing (Ducklow et al. 2007, Ducklow et al. 2013). Sea-ice is forming later in the season and retreating earlier (Vaughan et al. 2003, Ducklow et al. 2007). Throughout the Antarctic Peninsula region the winter ice season has decreased by one to two days per year on average with some areas experiencing a decrease of five days (Vaughan et al. 2003). In total, the length of the sea-ice season has shrunk approximately 92 days from 1979-80 to 2012-13 (Ducklow et al. 2013). Sea-ice is critically important in structuring WAP marine ecosystems (Ducklow et al. 2007, Ducklow et al. 2013).

There is already evidence that the warming has altered the food web (Ducklow et al. 2007). In areas that have experienced sustained warming and associated ice loss, salps (*Salpa thompsoni*) have replaced krill as the major phytoplankton consumer (Atkinson et al. 2004). Top predators such as Adélie (*Pygoscelis adeliae*) and chinstrap (*P. antarcticus*) penguins have shown marked declines throughout the WAP that are correlated with increasing temperatures and ice loss (Lynch et al. 2012). The changing sea-ice regime is likely influencing predator-prey dynamics and population dynamics at

all levels of the food web. Marine resource managers for the region may find it useful to explore how changes in the sea-ice regime will impact harvested and monitored species before making changes to fisheries management policies and strategies.

The software package Ecopath with Ecosim (EwE) was designed to facilitate the creation of dynamic food web models which can be used to aid in the development of fisheries policies, including the development of MPAs (Pauly et al. 2000, Christensen and Walters 2004). To explore fishing policy options, EwE requires a mass balanced food web model (Ecopath) and time dynamic simulations (Ecosim) that recreate observed trends of abundance. Spatial policies can be explored using Ecospace. There are two published EwE mass balanced food web models that overlap in whole or in part with the WAP: Cornejo-Donoso and Antezana (2008) and Ballerini et al. (2014). Two other EwE models have been made available in the grey literature (Erfran and Pitcher 2005, Hoover et al. 2012). All four models produced mass balanced Ecopath models. Neither of the two published models (Cornejo-Donoso and Antezana 2008, Ballerini et al. 2014) nor the models in the grey literature (Erfran and Pitcher 2005, Hoover et al. 2012) created time dynamic simulations models that successfully recreate observed trends of abundance.

The objective of this study is to create a mass balanced food web model, and time dynamic simulations that recreate observed trends of abundance for monitored species in the WAP. The work presented here evaluates the extent to which the changes in sea-ice cover explain observed variation by including the sea-ice regime as an environmental driver. This new model synthesizes the existing literature, and builds on previously published models (Erfran and Pitcher 2005, Cornejo-Donoso and Antezana 2008, Hoover

et al. 2012, Ballerini et al. 2014). In addition to exploring the role of sea-ice in influencing species biomass changes over time, this new mass balanced model representative of the WAP ecosystem will form the basis of a spatially dynamic food web model (Ecospace) to explore Marine Protected Area (MPA) placement options in future research (Chapter 4).

Methods

Study Area

To facilitate fisheries management, the Antarctic marine environment has been divided into statistical subareas. The study area is defined as the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Statistical Subarea 48.1. This is a region of the southwest Atlantic that includes the Western Antarctic Peninsula and South Shetland Islands (CCAMLR 2017). Statistical Subarea 48.1 has an area of approximately 630,279 km² (Hill et al. 2007) and is the portion of Antarctica closest to South America (Figure 1, Figure 2). The only currently operating commercial fishery in Statistical Subarea 48.1 is the krill fishery, which has removed an average of approximately 55,000 tonnes of krill a year since the 1987/88 fishing season (CCAMLR 2017). Recently the krill catch in Statistical Subarea 48.1 has been increasing with the catch exceeding 150,000 tonnes in three of the last six years (CCAMLR 2017). This level of catch approaches the trigger limit of 155,000 tonnes that would result in closure of the krill fishery for the season (CCAMLR 2016a).

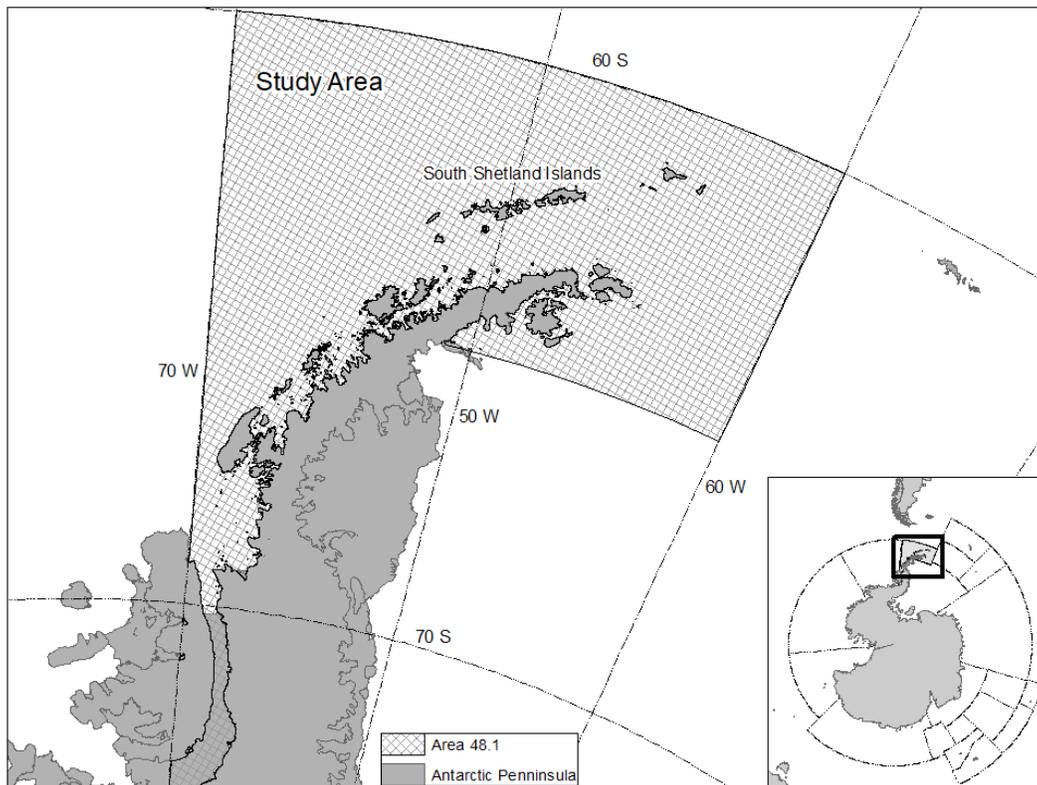


Figure 2. Study area detail.

Mass Balanced Food Web Model (Ecopath)

The food web model was created using the software package, Ecopath with Ecosim and Ecospace (EwE). EwE is open source, freely available software that has been used to model ecosystems worldwide (Pauly et al. 2000, Christensen and Walters 2004). Ecopath creates a mass balanced food web model of the ecosystem based on the assumption that predation, fishing pressure, and competition are critical to structuring the community (Pauly et al. 2000, Christensen and Walters 2004).

Ecopath relies on two master equations to parameterize the model. As described in Christensen and Walters (2004) the first equation describes the production term, P_i .

$$P_i = Y_i + M2_i \times B_i + E_i + BA_i + M0_i \times B_i \quad \text{Equation 1}$$

For each species i , Y_i is the total fishery catch, $M2_i$ is the instantaneous predation rate, B_i is the biomass, E_i is the net migration rate, BA_i is biomass accumulation, and $M0_i$ is ‘other’ mortality.

The predation term, $M2_i$, describes how predators and their prey relate to each other through the food chain for all predator groups j feeding on prey species i (Christensen and Walters 2004)

$$M2_i = \sum_{j=1}^n \frac{Q_j \times DC_{ji}}{B_i} \quad \text{Equation 2}$$

Where Q_j is the total consumption rate of predator group j and DC_{ji} is the proportion of predator j 's diet that species i comprises.

The ‘other mortality term’, $M0_i$, includes all other forms of mortality not described by predation or fishing pressure. It is internally calculated by Ecopath using the following equation:

$$M0_i = \frac{P_i \times (1 - EE_i)}{B_i} \quad \text{Equation 3}$$

Where EE_i is the ecotrophic efficiency or the proportion of production utilized in the system (Christensen and Walters 2004).

The second master equation describes the energy balance of each group such that

$$\textit{Consumption} = \textit{production} + \textit{respiration} + \textit{unassimilated food} \quad \text{Equation 4}$$

This equation requires that consumption of any one group is less than the production of the group, thus ensuring that the model remains in mass balance (Christensen and Walters 2004).

For this study, the food web of the WAP has been simplified and is represented by 35 functional groups, including a detritus group (see Appendix for definitions of the functional groups). Due to the importance of krill in the region (Constable et al. 2000, Ducklow et al. 2013, Ballerini et al. 2014), special focus was paid to krill and monitored krill predators. Species in the region that have been designated by the CCAMLR as indicator species (Agnew 1997, Constable 2002) are represented in the model as single species groups. It is the intention that this model will eventually be used to inform the MPA development process for the region. Therefore, all currently monitored species which are likely to be important in the final research and monitoring plan associated with the new MPA, were given their own single species groups. Other species, such as non-krill zooplankton, phytoplankton and fish species for which relatively little data exist, were combined into multi-species functional groups.

The modeled groups are meant to represent all levels of the food web from microscopic plankton to apex predators. Primary producers and non-krill zooplankton are represented by size based multi-species functional groups. Midlevel consumers are represented by several functional groups for zooplankton, fish and cephalopods. Krill are represented by a multistanza group, with one stanza for large krill which are older than two years and are typically large enough to reliably detect using fisheries acoustics (Pers. comm. A. Cossio, NOAA AMLR, May 2016) and another stanza for small krill, which are younger than two years old and includes sizes that are more challenging to detect during acoustic surveys. Similarly, “other euphausiids” which represent the very abundant species *Thysanoessa macrura* and *Euphausia crystallorophias* (Ballerini et al. 2014, Haraldsson and Siegel 2014) have been separated from the more generic size-based zooplankton groups. Preliminary stable isotope analyses indicate that these two species occupy a similar trophic level that is higher than the trophic level occupied by krill (Pers. comm., J. Walsh, NOAA AMLR, August 2016). Relatively little data describing specific fish species exist for the area. Previously published models group fish species into large multi-species groups, often making a single distinction between deep water myctophid fishes and all other species (for example see Hill et al. 2007, Ballerini et al. 2014). The model follows this convention, except for three on-shelf fish species for which times series abundance data are available, which were modeled as single species groups. *Champscephalus gunnari* and *Gobionotothen gibberifrons* were fished commercially in Statistical Subarea 48.1 until the populations suffered significant declines and caused the closure of those fisheries (McElroy 1984, Miller 1991, Constable et al. 2000). These

species have been the subject of several fisheries surveys (Kock and Jones 2005) and have a more robust data record than other fish species in the region. The same surveys also reported catches of *Notothenia rossii*. Birds and marine mammals are voracious krill predators and comprise the upper levels of the food web. Due to long-term monitoring and data collation efforts (Woehler 1993, Hinke et al. 2007, Lynch et al. 2012, Ducklow et al. 2013, Hinke et al. 2014), sufficient data exist to model each of the penguin species as single species groups. In contrast, the data record is sparse for flying seabirds, so these were grouped together in one functional group. All pinniped species known to inhabit the area were represented by single species groups. Ross seals were not included in this model as they occur irregularly and in very low numbers within the study area (Forcada et al. 2012). Cetaceans are represented by several single species groups that encompass the common residents of the area (Hedley et al. 2001, Mori and Butterworth 2006).

Specification of Ecopath Model Parameters

Initial biomass estimates were determined for all consumer groups using data collected during the period 1992- 2002 (

Appendix). Because data on the biomass of primary producers in the region are scarce, the biomass of phytoplankton and ice algae functional groups were calculated by the model. Following the advice of Heymans et al. (2016), the ecotrophic efficiency (EE) for primary producers in this largely pelagic ecosystem was set to 0.5, and the model estimated the required biomass for primary producer functional groups. For all other groups, the model calculated the EE. The base year of the model was set to 1996.

Two species of whales are known to be increasing in the study area (Branch 2011, Pastene and Hakamada 2016). However, robust time series to document these increases do not seem to currently exist. To account for the known increase, a bioaccumulation term of 3.9% per year was incorporated for Humpback whales (*Megaptera novaeangliae*). This is consistent with the reported estimated average humpback whale population growth for the region of 4.5% with a 95% confidence interval of -2.9% to 12.3% (Branch 2011). The model failed to balance if the bioaccumulation term was set higher than 3.9%. While annual growth rates have not been published for Fin whales (*Balaenoptera physalus*) in the study region, reported sightings data (Pastene and Hakamada 2016) reveal that fin whale sightings follow a similar, but slightly diminished pattern of increase as humpback whales. A bioaccumulation of 2.9% per year was used for Fin whales.

Production/ Biomass Ratio

The production to biomass ratio (P/B) describes the rate at which a trophic group can replace itself. It is therefore a measure of the population growth rate. This rate is poorly described for many lower trophic level species. Due to lack of data, the P/B ratios

for primary producers, sized classed zooplankton, salps, and benthic invertebrates were adopted from previously published models. Ballerini et al. (2014) estimated phytoplankton productivity from satellite imagery, estimated P/B for the “other euphausiid” functional group from studies conducted in Japan (Taki 2006), and estimated the P/B value for salps using ingestion rate data from Pakhomov (2004). These values were adopted into the current model.

Krill are included in the model as a multi-stanza functional group, which allows it to be modeled with multiple age classes. Krill are represented by two stanzas, one for animals older than 24 months (large krill) and second for animals younger than 24 months (small krill). Instead of P/B, base mortality (Z) is input for each stanza (Christensen and Walters 2004). The multi-stanza approach assumes that body growth for the species follows a Von Bertalanffy growth curve and that the species population as a whole has reached a stable age-size distribution (Christensen and Walters 2004). These assumptions seem valid for the Antarctic krill population (Rosenberg et al. 1986, Candy and Kawaguchi 2006). A recent review of published krill mortality rates indicate that temperature, age composition of the population, and sub region where the krill were sampled can significantly influence krill mortality rates; estimates range from 0.38 to 1.22 (Reiss 2016). Previously published Ecopath models for the region use a value of 1 (Cornejo-Donoso and Antezana 2008, Ballerini et al. 2014). Current CCAMLR modeling efforts indicate that a value of 0.8 is more appropriate to use for krill (Pers. comm., D. Kinzey, NOAA-AMLR, April 2015), and was used as the Z value for both large and small krill. This value, and the Von Bertalanffy curve curvature constant (K) of 0.440

were derived from the earlier work of Rosenberg et al. (1986) and of Candy and Kawaguchi (2006). The model derived the biomass of the small krill from the entered Z and K values and the biomass of large krill.

Mortality estimates for Antarctic fish are scarce (Kock and Jones 2005). Hill et al. (2007) compiled all known data regarding local fish species mortality (P/B ratio). The P/B value for myctophid fish was found to range between 0.86-1.14. The value of 1.1 was selected for the current model during the balancing process. Similarly, Hill et al. (2007) noted that the P/B of on-shelf species of fish ranged from 0.19-0.60 and recommended a value of 0.46, which was adopted in this model. A mortality value of 0.29 is recognized as the best estimate for *N. rossii* (Kock and Jones 2005). Iverson (1998) determined that the pre-exploitation natural mortality of *C. gunnari* ranged between 0.23-0.96. The CCAMLR modeling exercises have endorsed using the midrange value of 0.48 (Hill et al. 2007). A specific P/B value for *G. gibberifrons* could not be found in the literature. The species was included in Hill et al.'s (2007) assessment of the mortality for on-shelf fish species, therefore the current model uses a P/B of 0.46 for this species.

For upper level predators, the P/B ratio can be represented by annual adult mortality (Banse and Mosher 1980, Ballerini et al. 2014) and is a commonly published parameter (Appendix). For all marine mammal and penguin functional groups, a published value for survival or mortality was found in the literature. The P/B value for flying birds was calculated using a weighted average of annual survival for each species

included in the functional group. Weight was assigned in accordance with the relative abundance of the species as described by Ribic et al. (2011).

Production to Consumption Ratio

To create a mass balanced model, Ecopath uses an estimate of consumption (**Error! Reference source not found.** and **Error! Reference source not found.**). This estimate is often input to the model as either a production to consumption (P/Q) ratio or a consumption to biomass (Q/B) ratio. The P/Q ratio can be calculated as growth efficiency, or the product of the Assimilation Efficiency (AE) and Production Efficiency (PE; Ballerini et al. 2014). AE values can be found in the literature for many functional groups (**Error! Reference source not found.**). The PE values were derived from Townsend et al. (2003).

Table 1. Assimilation Efficiency (AE) and Production Efficiency (PE). All PE values were derived from Townsend et al (2003).

Functional Group	AE source	AE	PE	P/Q
Killer Whales	Lockyer (2007)	0.93	0.02	0.0186
Leopard Seals	Townsend et al. (2003), Ballerini et al. (2014)	0.89	0.02	0.0178
Weddell Seals	Townsend et al. (2003), Ballerini et al. (2014)	0.87	0.02	0.0174
Crabeater Seals	Priddle et al. (1998)	0.84	0.02	0.0168
Antarctic fur seals	Fadely et al. (1990)	0.88	0.02	0.0176
S Elephant Seals	Townsend et al. (2003), Ballerini et al. (2014)	0.87	0.02	0.0174
Sperm Whales	Townsend et al. (2003), Ballerini et al. (2014)	0.87	0.02	0.0174
Blue Whales	Lockyer (1981)	0.79	0.02	0.0158
Fin Whales	Lockyer (2007)	0.8	0.02	0.0160
Minke Whales	Lockyer (1981), Armstrong and Siegfried (1991)	0.84	0.02	0.0168

Humpback Whales	Lockyer (1981), Armstrong and Siegfried (1991)	0.84	0.02	0.0168
Emperor Penguins	Kirkwood and Robertson (1997)	0.7	0.02	0.0140
Gentoo Penguins	Adams et al. (1993)	0.72	0.02	0.0144
Chinstrap Penguins	Adams et al. (1993)	0.72	0.02	0.0144
Adélie Penguins	Adams et al. (1993)	0.72	0.02	0.0142
Macaroni Penguins	Adams et al. (1993)	0.72	0.02	0.0144
Flying birds	Townsend et al. (2003), Ballerini et al. (2014)	0.9	0.02	0.0180
Cephalopods	Townsend et al. (2003), Ballerini et al. (2014)	0.8	0.13	0.1040
Myctophids (off shelf)	Townsend et al. (2003), Ballerini et al. (2014)	0.8	0.13	0.1040
On-shelf fish	Townsend et al. (2003), Ballerini et al. (2014)	0.8	0.13	0.1040
<i>N. rossii</i>	Townsend et al. (2003), Ballerini et al. (2014)	0.8	0.13	0.1040
<i>C. gunnari</i>	Townsend et al. (2003), Ballerini et al. (2014)	0.8	0.13	0.1040
<i>G. gibberifrons</i>	Townsend et al. (2003), Ballerini et al. (2014)	0.8	0.13	0.1040
Salps	Pakhomov et al. (2006)	0.7	0.35	0.2450
Benthic invertebrates	Townsend et al. (2003), Ballerini et al. (2014)	0.58	0.35	0.2030
Large Krill	Pakhomov et al. (1997)	0.64	0.35	0.2240
Small Krill	Meyer et al. (2003)	0.84	0.35	0.2940
Other euphausiids	Pakhomov et al. (1997)	0.64	0.35	0.2240
Microzooplankton	Townsend et al. (2003), Ballerini et al. (2014)	0.8	0.25	0.2000
Mesozooplankton	Townsend et al. (2003), Ballerini et al. (2014)	0.7	0.35	0.2450
Macrozooplankton	Townsend et al. (2003), Ballerini et al. (2014)	0.8	0.35	0.2800
Small phytoplankton	Townsend et al. (2003), Ballerini et al. (2014)	1	1	1
Large phytoplankton	Townsend et al. (2003), Ballerini et al. (2014)	1	1	1
Ice algae	Townsend et al. (2003), Ballerini et al. (2014)	1	1	1

Diet Matrix

The diet matrix describes the trophic interactions of all functional groups in the model. Cannibalism was not allowed to occur for any group as it can cause instability (Steele and Ruzicka 2011, Ballerini et al. 2014). The diet matrix was informed by published diet composition studies and publicly available reports of prey choices (Appendix).

Killer whales (*Orcinus orca*) represent a single species that occurs in several ecotypes distinguished by diet (Pitman and Ensor 2003, Pitman and Durban 2010). At least two distinct ecotypes of killer whales occur in the WAP. Ecotype A, which feeds on minke whales (*Balaenoptera bonaerensis* and *B. acutorostrata*) and to a lesser extent elephant seals (*Mirounga leonina*), and the more abundant Ecotype B, which feeds on Pack ice seals and penguins (Pitman and Ensor 2003, Pitman and Durban 2010). Fish eating killer whales may also occur in the region (Pitman and Ensor 2003). As no detailed diet studies have been published for Antarctic killer whales, the diet presented in this study reflects what whales in the region have been observed eating and has been skewed to favor the more abundant Ecotype B.

A diet study of leopard seals (*Hydrurga leptonyx*) in the region (Casaux et al. 2009a) described a high percentage of krill and a variety of fish in this predator's diet. Observations from elsewhere in the study region indicate that consumption of Antarctic fur seal (*Arctocephalus gazella*) pups by leopard seals is a significant source of pup mortality (Boveng et al. 1998, Forcada et al. 2009, Goebel and Reiss 2014). The diet used in the Ecopath model includes consumption of fur seals.

Diet studies have been conducted for Weddell, crabeater, Antarctic fur and southern elephant seals in the region (Daneri et al. 2000, Daneri and Carlini 2002, Casaux et al. 2003;2006, Hückstädt et al. 2012a, Hückstädt et al. 2012b). Weddell seals primarily forage on fish (Casaux et al. 2006). Antarctic krill is a significant portion of the diet for crabeater and Antarctic fur seals (Casaux et al. 2003, Hückstädt et al. 2012a). Three diet studies have been conducted on southern elephant seals in the region and all three agree that both fish and cephalopods are dietary staples (Daneri et al. 2000, Daneri and Carlini 2002, Hückstädt et al. 2012b). However, the studies do not assign proportion of diet to cephalopods or fish species. In the current study, the diet of southern elephant seals is described as favoring cephalopods, with a significant portion of the diet coming from both myctophid fish and on-shelf fish.

Generalized cetacean diets were published by Pauly et al. (1998). Additionally, Kawamura (1978) published gut contents for some whale species caught during Antarctic commercial whaling. Sperm whales (*Physeter macrocephalus*) are generally known to favor cephalopod prey, supplemented by some fish prey (Pauly et al. 1998). Studies of baleen whale foraging in the Antarctic have highlighted the importance of krill in the diet (Kawamura 1978, Armstrong and Siegfried 1991, Santora et al. 2014). The diets of blue whales (*Balaenoptera musculus*), fin whales (*Balaenoptera physalus*), minke whales (*Balaenoptera bonaerensis* and *B. acutorostrata*) and humpback whales (*Megaptera novaeangliae*) were based on the generalized diets presented in Pauly et al (1998). However, the diets were adapted to recognize the importance of krill and other local

euphausiids as the main planktonic prey items (Kawamura 1978, Armstrong and Siegfried 1991, Santora et al. 2014).

Krill is an important component of the diet for all modeled penguin species and is especially important for pygoscelid (Adélie, Chinstrap, and Gentoo) penguin species (Lynnes et al. 2004, Polito et al. 2011). Proportion of krill in pygoscelid penguin diets varied in published reports from 68% (Polito et al. 2011) to over 99% (Lynnes et al. 2004). Krill comprised roughly half of the diet of Emperor penguins (*Aptenodytes forsteri*) (Klages 1989, Cherel and Kooyman 1998). Diet studies for Macaroni penguins (*Eudyptes chrysolophus*) indicate that approximately 70% of the diet is composed of euphausiids, including the species *Thysanoessa macrura* (Deagle et al. 2007). In this model, the euphausiid fraction of Macaroni penguin diet was split between krill and the other euphausiids functional groups.

The seabird functional group represents a diverse group of animals. There is wide variation in the reported diets of the species, though all species feed primarily in the near surface marine environment (Ainley et al. 1984, Ainley et al. 1994, Malzof and Quintana 2008). An attempt was made to synthesize the literature to create a representative diet for the functional group.

Cephalopods are known to be opportunistic foragers (Rodhouse and Nigmatullin 1996) and important consumers of myctophids and mesopelagic fishes (Kozlov 1995, Rodhouse and Nigmatullin 1996). The diet for this group was split between euphausiid and fish groups.

The fish functional groups represented in this model have diverse diets, but all groups include krill as a significant portion of their diets (Pakhomov et al. 1996, Barrera-Oro 2002, Flores et al. 2004, La Mesa et al. 2004, Pusch et al. 2004, Main et al. 2009, Casaux and Barrera-Oro 2013). *Electrona antarctica* was used as the example diet for myctophids as it is the best documented and most abundant myctophid in the region (Pusch et al. 2004, Ballerini et al. 2014).

Salps (*Salpa thompsonii*) are water column filter feeders (Perissinotto and A. Pakhomov 1998, Pakhomov et al. 2006). Their diet is comprised of both phytoplankton and zooplankton that are likely to be caught in their filters.

The diet of Antarctic krill (*Euphausia superba*) varies by both season (Perissinotto et al. 1997, Atkinson et al. 2002) and life stage (Meyer et al. 2002, Meyer et al. 2003). The diets presented in the current model takes that variability into account and attempts to reflect an average annual diet for both large and small krill groups.

Ballerini et al. (2014) re-created monthly diets for non-krill zooplankton based on published and previously non-published data. The diets for other euphausiids, microzooplankton, mesozooplankton, and macrozooplankton are derived from the average diets used in the Ballerini et al (2014) model. The diet for the other euphausiid group was adjusted to include more microzooplankton based on stable isotope analyses which indicate that other euphausiids occupy a higher trophic level than krill (Pers. comm. J. Walsh, NOAA-AMLR, August 2016).

The current model assumes that the benthic invertebrate functional group largely consumes detritus that has reached the benthos. This is consistent with other Antarctic food web models (Jarre-Teichmann et al. 1997, Ballerini et al. 2014).

Time Dynamic Simulation (Ecosim) set up

Ecosim allows for time dynamic simulations of the balanced model created in Ecopath. Its simulation outcomes indicate change in biomass of the groups based on the Ecopath model and applied environmental forcing functions. Ecosim employs coupled differential equations that are derived from the Ecopath Master Equation and are expressed as:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (MO_i + F_i + e_i) \times B_i \quad \text{Equation 5}$$

Where $\frac{dB_i}{dt}$ is the growth rate during time t of the biomass of group i, g_i is the net growth efficiency, Q_{ji} and Q_{ij} are the consumption rates, I_i is the biomass immigration rate and is assumed constant over time, MO_i is the mortality rate that is not associated with predation, F_i is the fishing mortality rate, and e_i is the emigration rate (Christensen and Walters 2004).

Consumption rates are based on a simple Lotka-Volterra predator prey model that has been modified to include “foraging arena” characteristics. The foraging-arena concept recognizes that prey can occur in states that are vulnerable to predation and states

that are not. Prey shift between the states as they seek to access resources like shelters that make them safer or seek food in areas that leave them more exposed. The different vulnerabilities of the prey can affect the consumption rate by predators (Christensen and Walters 2004). Consumption rates, Q_{ij} , are calculated as follows:

$$Q_{ij} = \frac{a_{ij} \times v_{ij} \times B_i \times B_j \times T_i \times T_j \times S_{ij} \times (M_{ij}/D_j)}{v_{ij} + v_{ij} \times T_i \times M_{ij} + a_{ij} \times M_{ij} \times B_j \times S_{ij} \times (T_j/D_j)} \quad \text{Equation 6}$$

Where a_{ij} is the effective search rate for i by j , v_{ij} is the vulnerability of the prey to prey (i) to predator (j), B represents the biomass for prey (i) and predator (j), T represents the relative feeding time for prey (i) and predator (j), S_{ij} is the forcing function, M_{ij} represents mediation, and D_j describes how handling time limits consumption rates.

Users can modify the Q/B ratio of consumer groups by applying a forcing function (S_{ij}) that describes an environmental parameter that influences trophic interactions. While not employed in the current model, Ecosim allows for the presence of a third species to impact the trophic interactions between consumers and prey. This is known as mediation and is represented in the equation by M_{ij} .

Ecosim input

Two types of data were used in the time dynamic simulations for the WAP. The first are time series that illustrate trends in abundance in eight monitored species for the

years 1996-2012. The second type of data are time series describing environmental conditions that likely influenced abundance trends during the same time period, called forcing functions. Forcing functions used in this model are measures of primary production, the sea-ice regime, and for one species, observed predation rates. The forcing functions were used to impact trophic interactions between specific predator and prey pairs, and a sea-ice index (described below) was used to drive the model for krill and *G. gibberifrons*. Using the sea-ice index to drive the model for these species essentially directly tied their patterns of biomass accumulation to sea-ice conditions. The shape of this response is described below, but in general the model was informed that biomass increased as sea-ice index increased.

Reliable, yearly time-series datasets dating back to at least the 1990s are available for five functional groups: Antarctic fur seals, Adélie penguins, Chinstrap penguins, Gentoo penguins, and Antarctic krill. Less regular time series data are available for three fish species: *N. rossii*, *C. gunnari*, and *G. gibberifrons* (Table 2). Both fisheries independent acoustic measurements and reported landings are available for krill. Abundance datasets for vertebrates represent counts of animals in discrete locations, krill data represent estimated density. All abundance data were entered into the model as “relative biomass” which informs the model to fit to trends, rather than specific values. Data prior to 1996 were not included in the Ecosim runs. This ensures that the time series data start at the same time as the base year for the Ecopath model.

Table 2. Relative biomass time series sources.

Model Groups	Time Series Source(s)	Notes
Antarctic fur seals	Goebel and Reiss (2014)	
Adélie Penguin	Hinke et al. (2007), Pers. Comm., J. Hinke, NOAA-AMLR., April 2015 and LTER (http://oceaninformatics.ucsd.edu/data/zoo/data/pallter/datasets)	Colony counts from the Southern LTER monitored colonies were added to the Northern NOAA-AMLR colonies to make the time series
Chinstrap Penguins	Hinke et al. (2007), Pers. Comm., J. Hinke, NOAA-AMLR, April 2015	
Gentoo Penguins	Hinke et al. (2007), Pers. Comm., J. Hinke, NOAA-AMLR, April 2015	
<i>N. rossii</i>	Kock and Jones (2005) and Kock and Jones (2012)	The time series was created by combining early data points published in the literature with more recent unpublished data points.
<i>C. gunnari</i>	Kock and Jones (2005) and Kock and Jones (2012)	The time series was created by combining early data points published in the literature with more recent unpublished data points.
<i>G. gibberifrons</i>	Kock and Jones (2005) and Kock and Jones (2012)	The time series was created by combining early data points published in the literature with more recent unpublished data points.
Large Krill	NOAA-AMLR (https://swfsc.noaa.gov/AERD-Data/)	

Ecosim allows environmental variables to influence biomass accumulation in the model via forcing functions. Forcing functions are time series of environmental variables that help the model better recreate observed trends of abundance. The forcing function mechanism makes it possible to explore the role of specific environmental variables in influencing biomass accumulation patterns in the ecosystem. Due to the documented importance of the sea-ice regime in influencing krill abundance and ecosystem dynamics (Atkinson et al. 2004, Ducklow et al. 2007, Ducklow et al. 2013), special attention was

paid to sea-ice forcing. Four forcing functions were used: chlorophyll *a* concentration, sea-ice area, open water area, and observed predation mortality rate of fur seal pups.

Palmer Long Term Ecological Research (LTER) scientists have been measuring chlorophyll *a* at Palmer Station weekly since 1995 (Schofield 2013). Due to equipment failures, there were several months of missing data. The long term monthly average was used as an approximation for the missing months of data. The chlorophyll *a* forcing function was applied to the primary producers. This caused primary production in the model to cycle with the observations from the real world.

Palmer LTER also makes available a time series of the monthly average sea-ice area in square kilometers and monthly average of open water area in square kilometers observable in the Palmer LTER study area. The sea-ice area is sensed by microwave satellite. Areas are considered “iced” when they have more than 15% ice cover (Stammerjohn 2013). Several species represented in the model are known to be directly or indirectly impacted by ice conditions in complex ways. Winter sea-ice is thought to positively influence penguin survivorship (Hinke et al. 2007, Trivelpiece et al. 2011). Krill, the most important prey item in the model, is known to be ice dependent, finding both predation refuges and food within the ice (Everson 2000). Initially, the unaltered sea-ice area dataset was incorporated in the model. However, that did not improve the fit of the model. A sea-ice index, described below, was made to identify “good ice years” and smooth some of this variability. Recalling the work of Hinke et al. (2007 and 2014), attempts were made to implement this new index focusing on winter ice conditions. However, the Palmer LTER sea-ice dataset did not exhibit sufficient variability in the

maximum winter sea-ice area. For many of the years, the entire LTER study area was covered in ice, and this measure could not be used to distinguish between years. Instead, the annual summer sea-ice area minimum was used to construct the sea-ice index. The assumption that years with greater sea-ice in the summer were generally icier throughout the year underlies the index. This may be a reasonable assumption as warmer summers are known to contribute to accelerating sea-ice loss by acting as a positive feedback loop (Meredith and King 2005, Stammerjohn et al. 2011, Ducklow et al. 2013); warmer, ice free waters become rapidly warmer as they more directly absorb the sun's rays. The Palmer LTER sea-ice area dataset was analyzed to determine the minimum monthly sea-ice area for each year. These annual sea-ice minima were then scaled using the average value. Years where the minimum monthly sea-ice area was greater than average were assigned values greater than one, while those below average were assigned values less than one. The scaled annual dataset (Figure 3) was used as the sea-ice forcing function in the model. The sea-ice area forcing function was applied in two distinct manners. In one application, it was used to impact specific predator-prey interactions to influence the prey's vulnerability to predation.

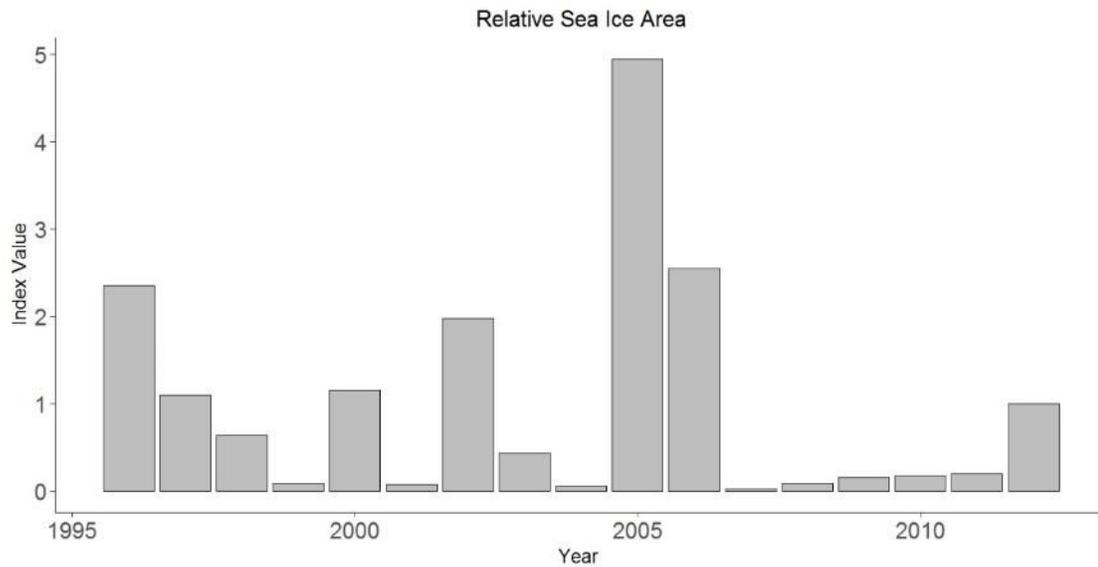


Figure 3. Relative sea-ice index.

Simply applying sea-ice index forcing to predator prey interactions was not sufficient to make the model recreate trends of abundance for large krill and *G. gibberifrons*. The sea-ice index was then used to drive the model for these species. When used to drive the model for a specific group, a functional response curve is needed to describe how that group responds to changes in the sea-ice index. Curves were fitted for both species independently, after forcing had been applied to predator prey interactions. Krill are known to exhibit declining abundance in areas that have experienced significant ice loss (Atkinson et al. 2004). Krill recruitment is higher following winters with high sea-ice extent (Siegel and Loeb 1995, Daly 2004, Reiss 2016). Data provided in the literature were not sufficient to directly construct a response curve for large krill. Recognizing that krill recruitment and abundance generally respond positively to increased sea-ice, a linear response curve and a sigmoidal curve were tested (

Figure 4). Fit of the model is measured by sum of square difference (SS) between observed value and simulation outcomes. The linear curve changed the SS for adult krill from 20.5 with no sea-ice driving to 11.69. Indicating that, indeed, krill in the model respond positively to increases in sea-ice. A sigmoidal response curve, with a very steep positive response further improved the SS of krill to 10.18, and slightly improved the fit for Adélie penguins, chinstrap penguins, gentoo penguins, *C. gunnari* and *G.*

gibberifrons. The total SS for the model, which includes SS values for the eight monitored species, differed by approximately four across trials using the sigmoidal response curve and the linear response curve. The trial with the sigmoidal curve had the smaller overall SS. Krill responding positively to increase in sea-ice agrees with the general patterns documented in the literature (Siegel and Loeb 1995, Atkinson et al. 2004, Daly 2004, Reiss 2016). The successful implementation of the both the linear and sigmoidal response curves illustrates how small changes in sea-ice index, based on annual minimum sea-ice, can have significant changes in krill population dynamics. The sigmoidal response curve was retained in the model as it gave a slightly better fit for the for krill and the three penguin species that are regularly monitored. The model fit for krill was improved further after the fit for *G. gibberifrons* was improved.

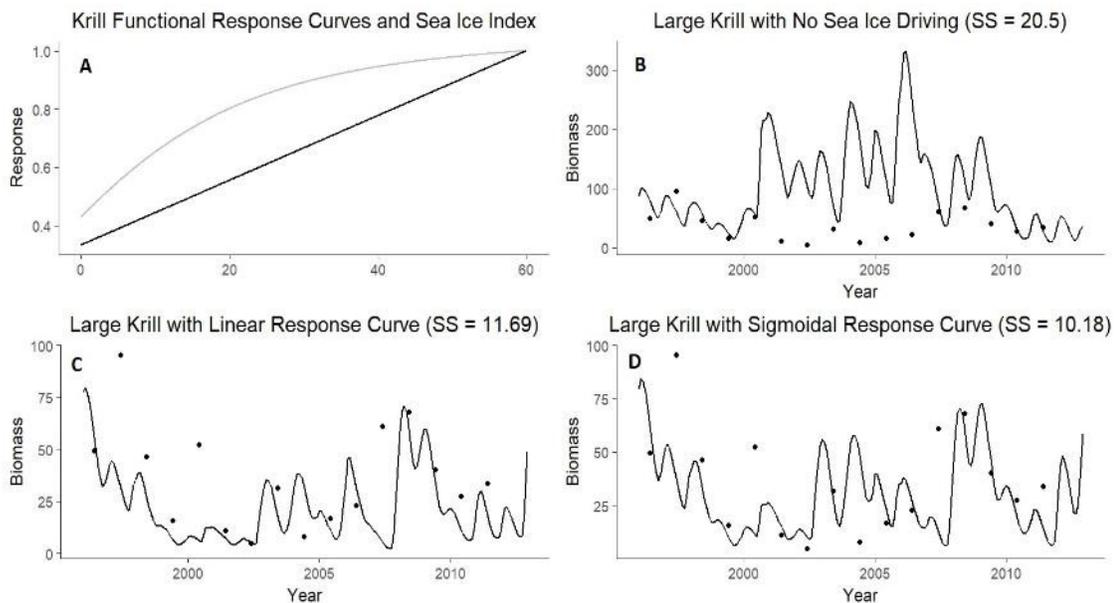


Figure 4 Krill Ecosim response curves. Panel A depicts linear functional response curve (black) and the sigmoidal response curve (grey) that were used to help the model recreate observed trends of abundance for large krill. The remaining three panels compare the model fit to observed values when no curve is applied (B),

the linear functional response curve is applied (C) and the sigmoidal functional response curve is applied (D). The sigmoidal functional response curve was retained.

G. gibberifrons is a benthic fish that breeds in the winter, and releases pelagic eggs (Barrera-Oro et al. 2000). The time series data indicate a fairly dramatic decline in the species (Kock and Jones 2005, Kock and Jones 2012). When initially implemented the model was unable to recreate this pattern, and instead indicated an increase in the species with an SS of 9.321. Applying forcing functions to foraging interactions between *G. gibberifrons* and its predators and prey failed to bring the model into line. This fish species dwells in the northern part of the study area and is not considered ice dependent (Barrera-Oro et al. 2000). However, because this animal breeds in the winter it is possible that it could respond positively to sea-ice, or oceanic conditions associated with sea-ice. As an experiment, the simulation was re-run with sea-ice driving the model for *G. gibberifrons* (Figure 5). As for krill, a linear curve was tried. Surprisingly, the simulation outcomes now aligned closely with the observed data. The SS decreased to 0.419, and the simulation outcome mirrored the decline of the species. Additionally, the fits for krill and other functional groups improved following the improvement in the fit of *G. gibberifrons*. Because a sigmoidal curve improved the fit for krill, a sigmoidal response curve was tried for *G. gibberifrons*. This decreased model performance, with the SS rising to 20.20. While it is unclear how this benthic fish is tied to the sea-ice regime, the model seems to indicate that sea-ice patterns, or oceanic conditions associated with sea-ice, influence the population dynamics for this species. The linear response curve was retained in the model.

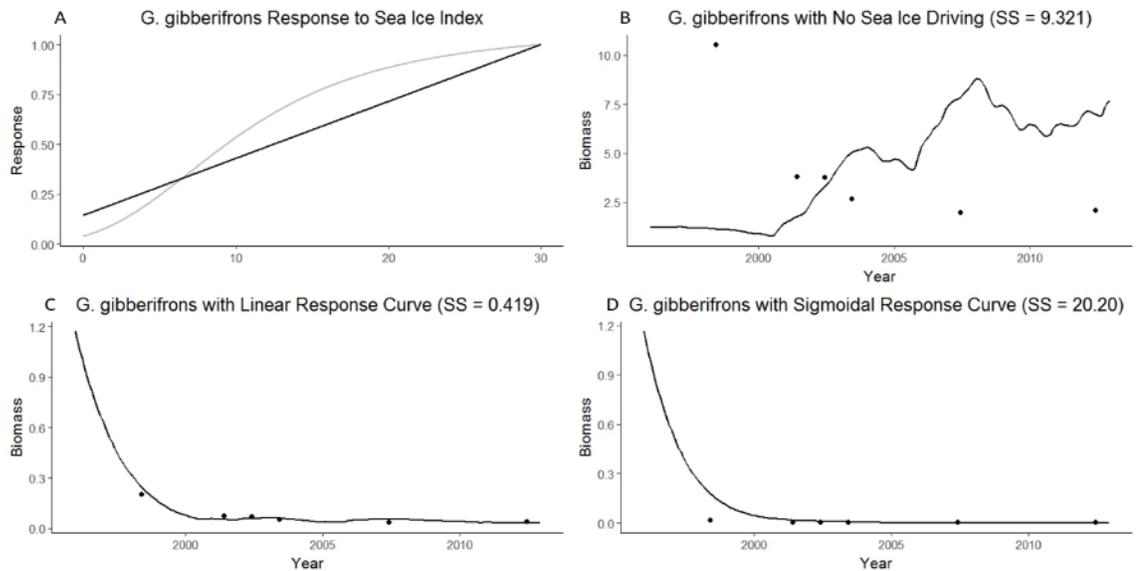


Figure 5. *G. gibberifrons* Ecosim response curves. Panel A depicts the linear functional response curve (black) and the sigmoidal response curve (grey) that were used to fit the model to observed trends of biomass for *G. gibberifrons*. The next three graphs compare the model fit to observed values when no curve is applied (B), the linear functional response curve is applied (C) and the sigmoidal functional response curve is applied (D). The linear functional response curve was retained. Please note that abundance time series data were entered into Ecosim as relative values and the model scaled appropriately. Panel B has a different y scale than panels C and D because of this scaling combined with the very different shape and trajectory of the simulation outcomes.

While some Antarctic species thrive in icy conditions, other species have increased success in open water conditions. Gentoo penguin populations have been increasing as the amount of sea-ice in the region declines (Hinke et al. 2007, Lynch et al. 2012). Similarly, Antarctic fur seals are pelagic predators that tend to aggregate in ice edge or open water environments to forage (Veit et al. 1993, Santora 2013). The average monthly open water area as described in the Palmer LTER data (Stammerjohn 2013) was used to force foraging interactions for pelagic species (Figure 6)

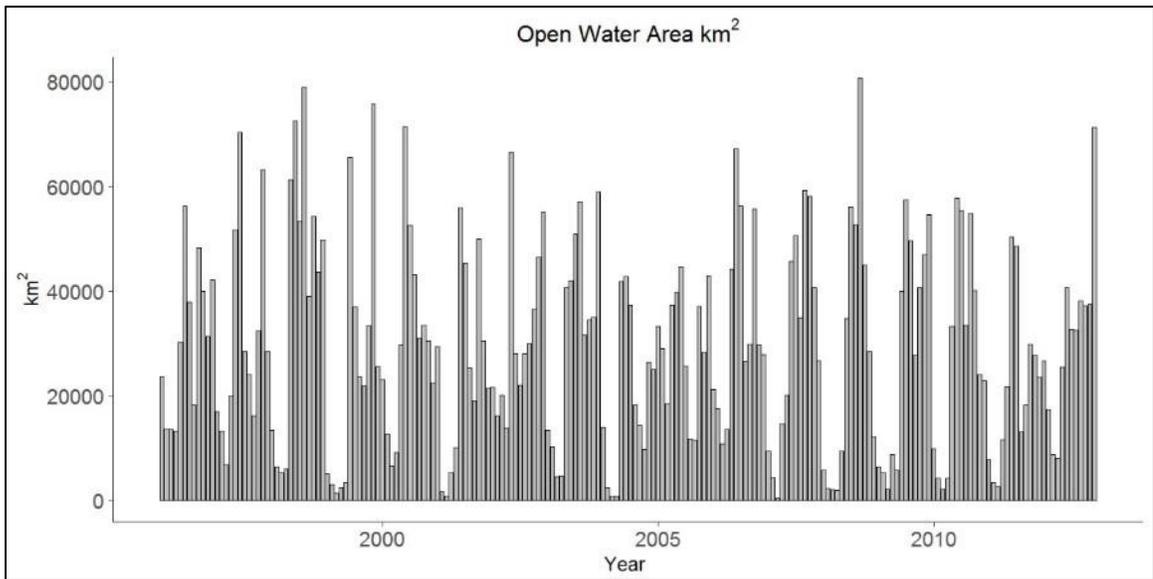


Figure 6. Open water area

Goebel and Reiss (2014) created a time series (Figure 7) of observed Leopard seal predation on Antarctic fur seal pups. These data were made available upon request and were used solely to force the trophic interaction between leopard seals and Antarctic fur seals.

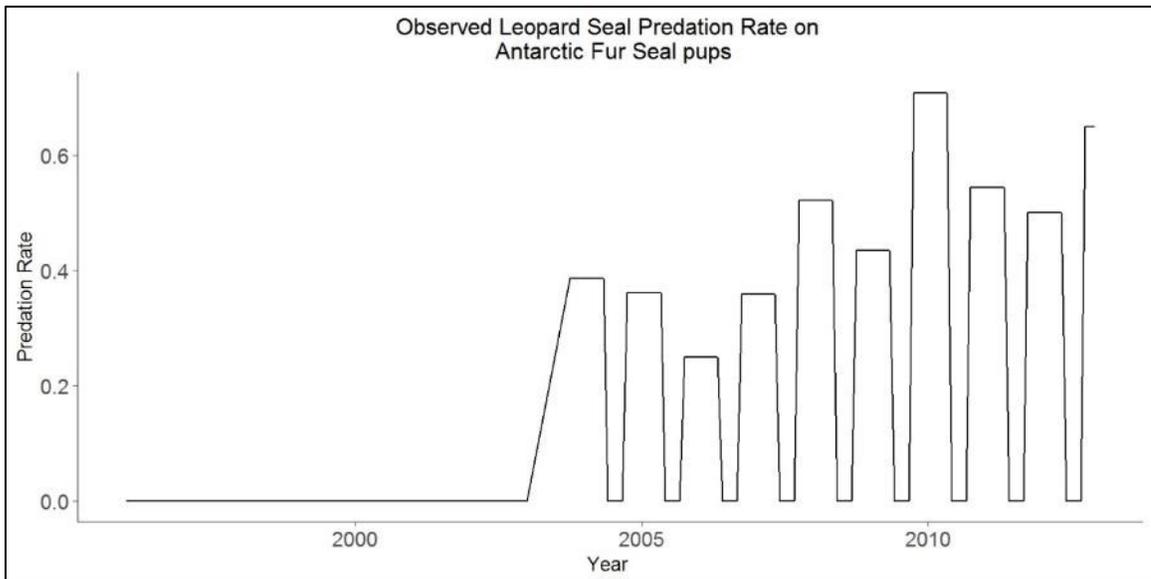


Figure 7. Observed Leopard seal predation rate on Antarctic fur seal pups. Figure recreated from Goebel and Reiss (2014).

Calibration of the Model

The model was initially run without applying any forcing functions. Under such conditions, the model failed to recreate observed trends of abundance for the eight monitored species. The chlorophyll *a* time series was applied to all primary producers to ensure that they cycled appropriately. Sea-ice and open water time series were applied to individual predator-prey interactions to influence the prey’s vulnerability to predation, the predator’s search rate, or the area searched. Choices of which time series were applied as forcing functions were influenced by the hunting strategies documented in the diet studies used to build the diet matrix. For example, gentoo penguins forage in near shore environments (Miller et al. 2010) and have been increasing in abundance as sea-ice has declined (Lynch et al. 2012). The open water environmental driver was used to force predator-prey interactions between gentoo penguins and on-shelf fish and also between

gentoo penguins and krill, making the prey items more vulnerable to gentoo predation in open water conditions. If applying a forcing function to a specific predator prey interaction did not improve the fit of the model, that function was no longer applied to that foraging interaction. Forcing improved the fit of the simulation outcomes for eleven predators. All retained predator-prey forcing is listed below in Table 3. Forcing function influence on predator prey interactions As described above, the sea-ice index was used to drive the model for both large krill and *G. gibberifrons*. This driving was applied after forcing on predator prey interactions failed to bring the simulation outcomes more in line with the observed data points.

Table 3. Forcing function influence on predator prey interactions.

Predator	Prey Forcing
Killer whales	Gentoo penguins vulnerability increases with open water
Leopard Seal	Fur Seals vulnerability increase with open water and observed predation rate; Chinstrap penguins vulnerability increases with sea-ice index; Myctophids vulnerability increases with sea-ice index
Weddell Seal	None
Crabeater Seal	None
Antarctic fur seals	Cephalopods vulnerability increases with open water; On-shelf fish vulnerability increases with open water; Large Krill search rate increases with sea-ice index
S Elephant Seals	None
Sperm Whales	None
Blue Whales	None
Fin Whales	None
Minke Whales	None
Humpback Whales	None
Emperor Penguins	On-shelf fish vulnerability and area increases with sea-ice index
Gentoo Penguins	On-shelf-fish vulnerability increases with open water; Large krill vulnerability increase with open water

Chinstrap Penguins	Myctophids vulnerability and search area increases with sea-ice index; On-shelf fish vulnerability and search area increases with sea-ice index; Large Krill vulnerability and search area increases with sea-ice index; Macrozooplankton vulnerability and search area increases with sea-ice index
Adélie Penguins	None
Macaroni Penguins	None
Flying Birds	None
Cephalopods	None
Myctophids	None
On-shelf fish	<i>C. gunnari</i> area increases with open water
N. rossii	Large krill vulnerability increases with open water; Other Euphausiids vulnerability increases with open water
C gunnari	Other Euphausiids vulnerability increases with open water
G. gibberifrons	None
Salps	None
Benthic invertebrates	None
Large Krill	Mesozooplankton vulnerability increases with sea-ice index; Large phytoplankton vulnerability and area increase with chlorophyll-a; Ice algae vulnerability and area increase with chlorophyll-a
Small Krill	Small phytoplankton vulnerability increases with sea-ice index; Large phytoplankton area increase with chlorophyll-a; Ice algae vulnerability and area increase with sea-ice index
Other Euphausiids	None
Microzooplankton	None
Mesozooplankton	None
Macrozooplankton	None

Sensitivity of the calibrated model was tested using the Monte Carlo (MC) routine provided by EwE (Christensen and Walters 2004). The MC routine randomly selects initial values of the input parameters (Biomass, P/B, and EE) using a coefficient of variation (C.V.) of 0.1. The MC runs attempt to find new combinations of input parameters that would further decrease the overall sum of squares for the model. The

degree of difference in the sum of squares between the user specified model, and the MC randomly selected runs is used to infer sensitivity. Twenty MC simulation trials were used to assess model sensitivity.

Results

Ecopath Model

The data described above were collated to create a mass balanced food web model for Statistical Subarea 48.1. When the model was initially implemented, with parameters taken directly out of the literature, several groups, including important prey species such as krill and on-shelf fish, had EE values significantly greater than 1. This indicated that demand was too high on those groups. Several of the diet studies used as references for the diet matrix had small sample sizes relative to the population and were spatially constrained in their sampling (for example Flores et al. 2004, Casaux et al. 2009a, Casaux et al. 2009b). It was assumed that the diets presented in these small or restricted area studies accurately represented the important prey items for each species, but that the percentage each item occupied was not exact. Diets were adjusted incrementally until the model was brought into balance. The final diet matrix is displayed in Table 4 and the balanced model is displayed in Table 5 below.

Table 4. Final diet matrix.

Functional Group	Prey
Killer whales	3% Leopard Seals, 46.5% Weddell Seals, 36.5% Crabeaters Seals, 1% Elephant Seals, 1% Blue Whales, 1% Fin Whales, 1% Minke Whales, 1% Humpback Whales, <1% Emperor Penguins, <1% Gentoo Penguins, 2% Chinstrap Penguins, <1% Adélie Penguins, 3% Myctophid fish, 2% On-shelf fish, <1% <i>N. rossii</i> , 1% <i>G. gibberifrons</i>
Leopard Seal	>1% Antarctic fur seals, >1% Gentoo Penguins, 3% Chinstrap Penguins, 7.8% Cephalopods, 4% Myctophids, 15% <i>G. gibberifrons</i> , 70% Large Krill
Weddell Seal	80% Cephalopods, 5% Myctophids, 60% On-shelf fish, 22% <i>G. gibberifrons</i> , 5% Benthic invertebrates
Crabeater Seal	7.5% Cephalopods, 7.5% Myctophids, 7% Onshelf fish, 78% Large Krill
Antarctic fur seals	1% Gentoo Penguins, 3% Chinstrap Penguins, >1% Adélie Penguins, >1% Macaroni Penguins, 5.4% Cephalopods, 20% Myctophids, 20% On-shelf fish, 50% Large Krill
S Elephant Seals	60% Cephalopods, 10% Myctophids, 14% On-shelf fish, 10% <i>N. rossii</i> , 6% <i>G. gibberifrons</i>
Sperm Whales	85% Cephalopods, >1% Myctophids, 4.5% On-shelf fish, 10% Benthic invertebrates
Blue Whales	61% Large Krill, 20% Other euphausiids, 19% Macrozooplankton
Fin Whales	1.5% Myctophids, 1.5% On-shelf fish, 71% Large Krill, 12% Other euphausiids, 1% Mesozooplankton, 13% Macrozooplankton
Minke Whales	1% Myctophids, 1% On-shelf fish, 76% Large Krill, 11% Other euphausiids, 11% Macrozooplankton
Humpback Whales	6% Cephalopods, 4% Myctophids, 4% On-shelf Fish, 76% Large Krill, 1.5% Mesozooplankton, 8.5% Macrozooplankton
Emperor Penguins	10% Cephalopods, 38% On-shelf Fish, 52 % Large Krill
Gentoo Penguins	10% Myctophids, 10% On-shelf-fish, 80% Large Krill
Chinstrap Penguins	2.25% Myctophids, 2.25% On-shelf Fish, 95% Large Krill, >1% Macrozooplankton
Adélie Penguins	1.25% Myctophids, <1 % <i>C. gunnari</i> , 1.25% <i>G. gibberifrons</i> , 96.2% Large Krill, 1.25% Macrozooplankton
Macaroni Penguins	1% Cephalopods, 10% Myctophids, 12% On-shelf Fish, 34% Large Krill, 35% Other euphausiids, 8% Mesozooplankton
Flying Birds	46% Cephalopods, 4.3% Myctophids, 8.7% On-shelf fish, 30% Large Krill, <1% Mesozooplankton, 10.5 % Macrozooplankton

Cephalopods	2% Myctophids, 2% On-shelf Fish, 21% Benthic invertebrates, 40% Large Krill, 15% Other euphausiids, 20% Macrozooplankton
Myctophids	25% Large Krill, 35% Other euphausiids, 5% Mesozooplankton, 35% Macrozooplankton
On-shelf fish	5.5% Cephalopods, 2% Myctophids, 1.5% <i>C. gunnari</i> , 1% Salps, 20% Benthic Invertebrates, 25% Large Krill, 13.5% Other Euphausiids, 8.5% Mesozooplankton, 23% Macrozooplankton
<i>N. rossii</i>	10% Myctophids, 2% Salps, 2% Benthic invertebrates, 60% Large Krill, 20% Other euphausiids, 6% Ice algae
<i>C. gunnari</i>	1% Myctophids, 90% Large Krill, 8% Other euphausiids, 1% Macrozooplankton
<i>G. gibberifrons</i>	1% Cephalopods, 2% Myctophids, 17% Salps, 59% Benthic invertebrates, 9% Large Krill, 2% Macrozooplankton, 10% Ice algae
Salps	<1% Small Krill, 10.4% Microzooplankton, 3% Mesozooplankton 41.5% Small phytoplankton, 45% Large phytoplankton
Benthic invertebrates	100% Detritus
Large Krill	10% Mesozooplankton, 50% Large phytoplankton, 10% Ice algae, 30% Detritus
Small Krill	10% Microzooplankton, 27.5% Small phytoplankton, 27.5% Large phytoplankton, 25% Ice algae, 10% Detritus
Other Euphausiids	20% Mesozooplankton, 60% Large phytoplankton, 20% Detritus
Microzooplankton	60% Small phytoplankton, 25% Large phytoplankton, 15% Detritus
Mesozooplankton	3% Microzooplankton, 24% Small phytoplankton, 66% Large phytoplankton, 7% Detritus
Macrozooplankton	1% Large Krill, 2% Small Krill, 1% Other euphausiids, 50% Mesozooplankton, 10% Small phytoplankton, 21% Large Phytoplankton

Table 5. Balanced Ecopath model. Values in parentheses were calculated by the model. Values marked with a * are Z values entered into the multi stanza for krill.

Functional Group	B (t/km2)	P/B	Q/B	EE	Trophic Level
Killer Whales	0.007524	0.02	1.075269	(0)	(4.723415)
Leopard Seals	0.008352	0.27	15.16854	(0.10763)	(3.405403)
Weddell Seals	0.081212	0.08	4.597701	(0.57904)	(4.157911)
Crabeater Seals	1.097774	0.1	5.952381	(0.0269)	(3.360988)
Antarctic Fur Seals	0.001032318	0.17	9.659091	(0.721891)	(3.692048)
S Elephant Seals	0.001035257	0.21	12.06896	(0.372133)	(4.229149)
Sperm Whales	0.02839939	0.29	16.66667	(0)	(4.115418)
Blue Whales	0.0071769	0.04	2.531646	(0.281818)	(3.210447)
Fin Whales	0.0428043	0.0315	2.55	(0.060002)	(3.209849)
Minke Whales	0.0472752	0.095	5.654762	(0.018014)	(3.188475)
Humpback Whales	0.08118936	0.04	2.380952	(0.024912)	(3.304195)
Emperor Penguins	0.000115949	0.1945	13.89286	(0.003587)	(3.670052)
Gentoo Penguins	0.001161069	0.22	15.2777	(0.949677)	(3.341648)
Chinstrap Penguins	0.02142	0.22	15.2778	(0.904332)	(3.158981)
Adélie Penguins	0.00583	0.12	36.61972	(0.117521)	(3.135117)
Macaroni Penguins	0.000114505	0.11	7.638889	(0.791649)	(3.449476)
Flying birds	0.004	0.088	4.888889	(0)	(3.826953)
Cephalopods	2.49	3.15	30.28846	(0.292114)	(3.235967)
Myctophids	3.27	1.1	10.58	(0.751568)	(3.295382)
On-shelf fish	5.25	0.46	4.423077	(0.92696)	(3.297093)
N. rossi	0.138	0.29	2.788	(0.032234)	(3.175258)
C gunnari	0.9	0.48	4.615385	(0.806537)	(3.127735)
G gibberifrons	1.2	0.46	4.423077	(0.189579)	(2.981859)
Salps	240	3	12.245	(0.001586)	(2.136)
Benthic invertebrates	85.5375	0.5	2.19	(0.553846)	(2)
Large Krill	81.26	*0.8	3.57	(0.9709627)	(2.103)
Small Krill	(28.93069)	*0.8	6.512725	(0.397018)	(2.1)
Other Euphausiids	148	1.5	6.6964	(0.135753)	(2.206)
Microzooplankton	25	55	275	(0.291669)	(2)
Mesozooplankton	130	4.81	19.63265	(0.760187)	(2.03)
Macrozooplankton	35	2.5	8.92857	(0.374296)	(2.56009)
Small phytoplankton	(161.0721)	75		0.5	(1)
Large phytoplankton	(148.8752)	75		0.5	(1)
Ice algae	(3.066724)	50		0.5	(1)
Detritus	5.77			(0.104473)	(1)

Ecosim

Time dynamic simulations were run for the seventeen-year period 1996-2012. When forcing functions were applied, the model could recreate trends of abundance for the eight groups for which observations are available; simulation outcomes closely tracked observed data (Figure 8). Sums of squares difference for each functional group ranged from less than 0.5 to 10.06 in the final fit model. Functional groups for which yearly data points were available, and which demonstrated an obvious trend in the abundance had the smallest SS values. The highest SS (10.06) was associated with large krill which had high variability in the time series data and lacked an obvious trend in abundance. Krill data were entered into the model without any smoothing because krill abundance is known to be highly variable both temporally and spatially (Nicol 2006, Santora et al. 2009). While the model was not able to recreate all the variability evident in the krill dataset, the simulation outcome was a reasonable approximation of krill's temporal dynamics in Statistical Subarea 48.1.

The total sum of squares for the model without forcing was 70.77 and simulation outcomes did not align with observed trends in biomass (Figure 8). After sea-ice forcing and driving of krill and *G. gibberifrons* were applied, the simulation outcomes much more closely recreated observed trends in the data. The SS for krill alone decreased nearly 50% from 19.71 to 10.06. The total SS dropped to 25.31 and the simulation outcomes much more closely matched the observed data (Figure 8). However, even though the overall SS dropped considerably, the fit for the species *C. gunnari* worsened after sea-ice forcing and driving was applied (Figure 8). The decrease in SS by 65% highlights the importance of the sea-ice regime in structuring the marine ecosystems of

Statistical Subarea 48.1. This finding agrees with long-term ecological studies in the area (Ducklow et al. 2007, Ducklow et al. 2013).

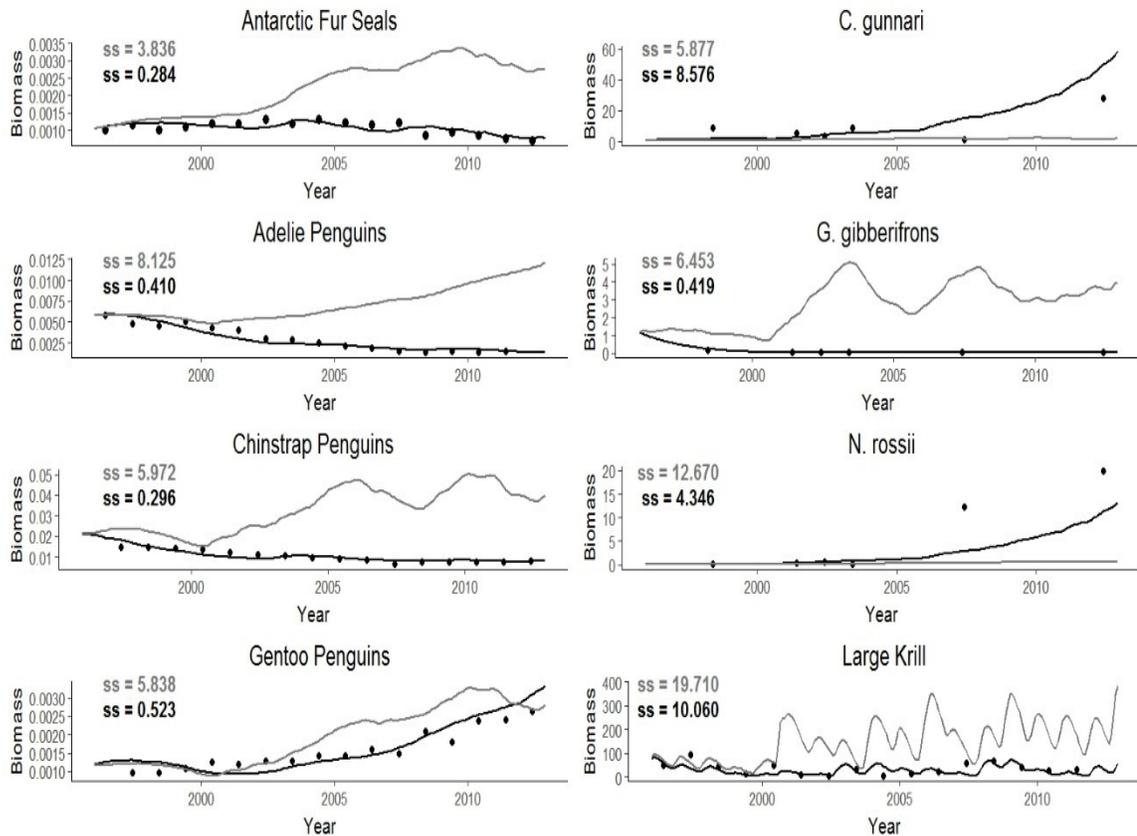


Figure 8. Results of Ecosim simulations. Abundance time series are plotted as black points. The relative biomass outcomes from the model are plotted as lines. Simulations without sea-ice forcing are shown in grey; simulations with sea-ice forcing are shown in black. The sum of squares (SS) difference between simulation outcomes and observed data are shown for each species.

The MC sensitivity analysis yielded 20 simulations that produced balanced models. The total combined SS value for each simulation varied between 23.72 and 44.03. The groups that exhibited the highest variability and contributed most to the SS, and thus are the most sensitive to the input parameters, were the two fish species *N.rossii*

and *C. gunnari* (**Error! Reference source not found.**). MC simulations identified a slightly better overall SS than that achieved in the model calibration process. This better fit was achieved on runs where the adjusted input parameters resulted in better fitting simulation outcomes for *C. gunnari*.

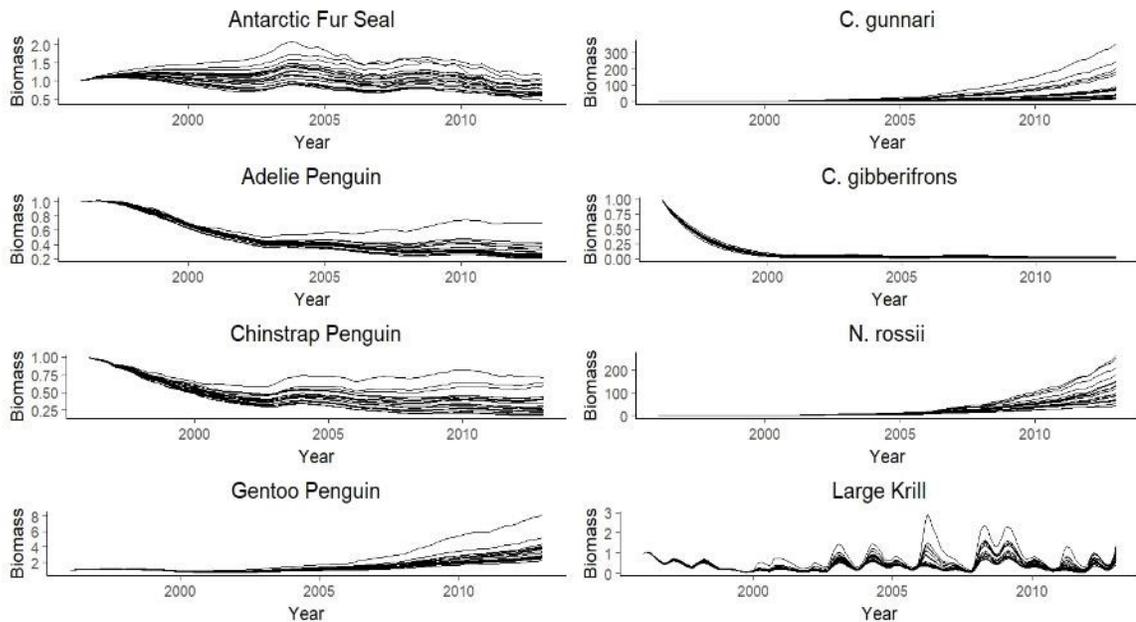


Figure 9 Results of Monte Carlo trials. Each line represents the biomass trajectory of that species over the course of a single trial. Note that the y scales for *N. rossii* and *C. gunnari* are two orders of magnitude larger than the scales for the other species. This indicates much higher sensitivity and uncertainty for these two species.

Discussion

The mass balanced food web model and time dynamic simulations described in this chapter represent a simplified version of the marine ecosystems of the WAP. The population trends described by the abundance datasets and recreated by the model are consistent with regional trends. The significant decline of Adélie and Chinstrap penguins

and increasing abundance of Gentoo penguins has been described throughout the WAP (Lynch et al. 2012). Similarly, the sharp decline in *G. gibberifrons* and increase in *N. rossii* was first described in 2007 (Barrera-Oro and Marschoff 2007) and has been updated in this model with the inclusion of more recent unpublished data (Kock and Jones 2012). The model has been calibrated and successfully recreates observed trends of abundance for key monitored species. The calibration of the model represents a significant advancement over the prior published uncalibrated EwE models for the region (see: Hoover et al. 2012, Ballerini et al. 2014). The Monte Carlo sensitivity analysis revealed that two fish species (*C. gunnari*, and *N. rossii*) were responsible for the greatest variability between runs. This result is unsurprising because population dynamics and diet data for these fish species are scarce in the literature (Kock and Jones 2005, Hill et al. 2007) and there are large gaps in the abundance time series.

This model illustrates the importance of the sea-ice regime in explaining the population dynamics for some monitored species. It has been well documented in the literature that changes in the sea-ice regime influence patterns of distribution and abundance of species in the WAP (Atkinson et al. 2004, Hinke et al. 2007, Lynch et al. 2012, Ducklow et al. 2013). Inclusion of the influence of the sea-ice regime allowed the model to recreate observed trends of abundance and improved the fit of the model to field observations and decreased SS by approximately 65%. Further, identifying specific predator prey interactions that are influenced by sea-ice conditions and creating sea-ice response curves for krill and *G. gibberifrons* make this model useful for exploring potential impacts of climate change on biomass accumulation patterns in the WAP.

Sea-ice in Dynamic Simulations

Current climate models indicate that sea-ice loss will continue (IPCC 2013).

Successful management of the WAP in the future will depend on understanding and predicting how species will respond to changes in the sea-ice regime. The simulation presented here investigated the role of temporal sea-ice dynamics on biomass accumulation patterns by using aspects of the sea-ice regime to force predation interactions and to drive the model for large krill and the fish, *G. gibberifrons*.

The sea-ice index used here is a normalized relative measure of annual minimum sea-ice area. Previous studies have indicated that it is the winter maximum sea-ice that is most important in determining krill predator recruitment (Hinke et al. 2007, Hinke et al. 2014). While summer sea-ice minima were used in the present study, the model presented here does not contradict those earlier findings. Sea-ice loss is impacted by a positive feedback loop of ice free waters absorbing more solar radiation and warming faster, (Meredith and King 2005, Stammerjohn et al. 2011, Ducklow et al. 2013), summers following colder icier winters are therefore likely to be colder and icier. The Hinke et al. (2007) study was focused on the northern part of WAP where there seems to be more winter sea-ice variability than is recorded in the Palmer LTER data set. Both the current modeling effort and Hinke et al (2007) reach the same conclusion that seasonal sea-ice dynamics, whether lagged winter maxima in the north or normalized summer minima in the south, influence krill and penguin abundance.

Krill are well known to be ice dependent (Everson 2000, Atkinson et al. 2004, Mori and Butterworth 2006) and to have increased population size following years of increased winter sea-ice extent (Siegel and Loeb 1995, Atkinson et al. 2004, Daly 2004,

Reiss 2016). However, previous studies described more general response patterns and were not sufficient to create a response curve to sea-ice concentration. This study presents a well-fitting curve that describes krill's response to sea-ice concentration which can be used to anticipate krill biomass patterns in response to summer sea-ice minima. This model can now be used to indicate how krill might respond to future changes in the sea-ice regime as the area continues to warm. Similarly, a sea-ice response curve was identified for *G. gibberifrons* that allowed the model to recreate observed trends of abundance for this fish. A direct link between this species and sea-ice has not been noted in the literature. While the sea-ice response curve works in the model, it may be representing effects of other (environmental) drivers that have not been well documented for the species.

Forcada et al. (2006) indicate that sea-ice conditions alone are unlikely to be responsible for penguin population dynamics patterns and suggest that changes in trophic dynamics in response to ice patterns may play an important role. The model presented in this study supports Forcada et al's (2006) finding. The model was only able to recreate observed trends of abundance when the sea-ice regime was used simultaneously to drive the model for krill and to influence predator prey dynamics for eleven predators. Ecosim simulations indicate that trophic interactions indirectly influence biomass accumulation patterns for roughly one third of the model groups spread across trophic levels. This suggests that sea-ice influence of trophic interactions may have broader impact than what is suggested by the penguin focused Forcada et al. (2006) study. The results of the time

dynamic simulations indicate that the role of sea-ice in structuring the WAP marine ecosystem is both central and complex.

Management Applications for the Model

The model is ready to be applied to evaluating the effects of future sea-ice regime. Theoretical future ice scenarios that utilize different levels of ice loss can be entered into the model to explore potential effects of climate change on biomass accumulation. Some species, such as the commercially fished Antarctic krill are known to be ice dependent (Everson 2000) , and are therefore expected to decline with ice loss (Atkinson et al. 2004). The model can help explore how a decrease in krill biomass could impact the biomass of krill predators and other species less directly connected to krill through the food web. This is of relevance to the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), the international governing body responsible for managing Antarctic marine living resources. The CCAMLR has long recognized that understanding ecosystem structure and process is essential to managing a sustainable krill fishery (Miller 2002). Recently, the CCAMLR agreed that creating a representative system of marine protected areas could help them both conserve Antarctic marine biodiversity and aid in the management of sustainable fisheries (CCAMLR 2011d).

Article II of the CAMLR Convention requires that the CCAMLR adopt an ecosystem based management (EBM) strategy for fisheries (McElroy 1984, Constable et al. 2000). The CCAMLR has long recognized the value of spatially allocating catch as part of EBM, and has pursued measures to disperse krill catch to avoid disproportionately impacting central place foragers as (Constable et al. 2000). Specifically, the CCAMLR

has divided Statistical Area 48 into Small Scale Management Units (SSMUs), eight of which are contained within Statistical Subarea 48.1, to help allocate catch as fishing pressure increases (Constable 2002;2011). Elsewhere in the Antarctic, the CCAMLR has subdivided Statistical areas into small scale research units (SSRUs), and has used time limited closures of selected SSRUs to manage active fisheries. In the Ross Sea Region, seven of the fifteen SSRUs were closed to fishing (CCAMLR 2011a;b) before transitioning spatial management of the region to a large, longer lasting, marine MPA (CCAMLR 2016b). MPAs therefore seem to be the logical extension of the CCAMLR's previous spatial management efforts. Careful design and successful implementation of an MPA would allow the CCAMLR to develop and articulate conservation goals that further EBM, beyond simple spatial allocation of catch.

The CCAMLR has identified the Western Antarctic Peninsula and Scotia Sea as an area ripe for developing an MPA (CCAMLR 2011d). The CCAMLR has also adopted a framework for the establishment of future MPAs (CCAMLR 2011c) This framework stipulates that MPAs should be created using the best available science and that they should aim to protect key ecosystem processes, among other protection objectives. Trophic interactions affect biomass accumulation patterns and are important ecosystem processes to consider for protection. In the face of sustained warming and continued sea-ice loss (Ducklow et al. 2007, Ducklow et al. 2013), it could be useful to consider dynamic trophic interactions when planning an MPA.

The new model described in this paper was designed to aid in the MPA planning process for the region. The functional groups in the present model include single species

groups for all species in the region that have been designated by the CCAMLR as indicator species (Agnew 1997, Constable 2002). These species will likely be important as the CCAMLR Members set conservation goals during the MPA planning process and develop a monitoring and management plan. The food web model and time dynamic simulations presented here lay the foundation for developing a spatial model that could explore MPA placement while considering the dynamic sea-ice regime and trophic interactions.

Summary and Conclusions

The new model presented here was successful in recreating observed trends of abundance when using sea-ice forcing functions. The sea-ice regime influences population dynamics both directly (krill and *G. gibberifrons*) and indirectly through trophic interactions involving eleven different predators. Including the sea-ice regime influence significantly improved the fit of the model and reduced the SS difference by approximately 65%. Because sea-ice influence is incorporated into the model it can be used to explore the effects of theoretical future sea-ice scenarios. The model has all currently monitored species in the region represented as single species groups, is calibrated, and has established how biomass of the modeled species responds to the sea-ice regime. This model is appropriate to develop into a spatio-temporal model to aid in the MPA design process for this rapidly warming region.

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CHAPTER THREE: EXPLORING POTENTIAL IMPACTS OF FUTURE SEA-ICE LOSS AND INCREASING FISHING USING TIME DYNAMIC AND SPATIO-TEMPORALLY DYNAMIC SIMULATIONS

Introduction

Since sea-ice records began in the 1970's, the Western Antarctic Peninsula region (WAP) has experienced significant declines in sea-ice extent and duration, and significant changes in the timing of sea-ice formation and melting (Vaughan et al. 2003, Ducklow et al. 2007, Stammerjohn et al. 2008, Stammerjohn et al. 2011, Trivelpiece et al. 2011, Ducklow et al. 2013, Stammerjohn 2013). It is likely that warming conditions (IPCC 2013) and sea-ice loss (Flores et al. 2012, Ducklow et al. 2013) will persist in the future, resulting in an increased number of low-ice or even ice-free years (Stammerjohn et al. 2008, Reiss et al. 2017). Changes in zooplankton communities (Atkinson et al. 2004, Atkinson et al. 2009, Ducklow et al. 2013) and penguin species distribution patterns (Lynch et al. 2012) have already been correlated with sea-ice loss and show strong spatial patterns. The more northerly, and consequently warmer, parts of the WAP have exhibited the greatest amount of change (Lynch et al. 2012, Ducklow et al. 2013). Antarctic krill (*Euphausia superba*), a key prey item and the target of the largest fishery in the region, has exhibited a biomass decline and shift in distribution patterns that is associated with sea-ice loss (Atkinson et al. 2004, Atkinson et al. 2009). Changes in krill abundance and spatial distribution may have cascading impacts for krill dependent predators, the krill

fishery, and the distributions of both. There is some indication that reduced availability of krill may be contributing to krill predator declines (Trivelpiece et al. 2011).

While sea-ice provides habitat for krill, and foraging areas for krill predators, it also acts as a barrier to fishing vessels. Heavily iced waters can cause damage to vessels and gear and are avoided (Antarctic Ecosystem Research Division Southwest Fisheries Science Center and NOAA Fisheries 2016). Following years of progressive sea-ice loss, and later onset of the winter sea-ice season, the krill fishery is now able to operate much later in the year (Kawaguchi and Candy 2009, Nicol et al. 2012). The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) has managed the fishery conservatively, utilizing both a total allowable catch and a precautionary trigger limit that is approximately eleven percent of the total allowable catch (CCAMLR 2010). The trigger limit forces fishing to cease for the season so as not to disproportionately impact central place foragers (Constable and Nicol 2002). The CCAMLR Conservation Measure (CM) 51-07 came into effect in 2009 and allocated no more than 25% of the trigger limit, or 155,000 tonnes to statistical area Statistical Subarea 48.1 (CCAMLR 2016). Catches of krill have increased in recent years (Nicol et al. 2012), with catches from the 2012/13 through 2014/15 season approaching or reaching the trigger limit (CCAMLR 2017). It is likely that in future years there will be interest in fishing beyond the trigger limit. It is also likely that as ice recedes, new areas will open to the fishery which may change the spatial overlap between krill predators and the fishery (Nicol et al. 2012, Reiss et al. 2017).

The CCAMLR has long considered that the spatial distribution of the fishery is an important factor in determining the fisheries impact on krill predators (Constable 2011). Small Scale Management Units (SSMUS) (Kock 2007) and the designation of the trigger limit (CCAMLR 2016) are tools that the CCAMLR has developed to distribute fishing efforts and reduce local impacts. Most recently, the CCAMLR has been pursuing the establishment of Marine Protected Areas (MPAs) as another tool to manage the spatial footprint of fisheries in Antarctica (CCAMLR 2011, Brooks et al. 2016) . The krill fishery's spatial pattern has changed over time (Kawaguchi et al. 2006, Kawaguchi and Candy 2009), and it is likely that as ice conditions change, and new areas become accessible to the fleet, the spatial distribution of fishing will continue to change. In order to continue to manage the krill fishery conservatively and effectively into the future, the CCAMLR will need to consider how sustained sea-ice loss affects both the total amount of krill available and the spatial distribution patterns of krill, their predators, and fishers.

The software package Ecopath with Ecosim allows for spatially- and temporally dynamic simulations to evaluate the impact of changes in environmental drivers and changes in fishing policies (Christensen and Walters 2004). In Chapter 2, an Ecopath model and Ecosim simulations were developed that recreate observed trends of abundance for eight monitored species. The calibrated model is therefore ready to evaluate how future changes in the sea-ice regime or fishing pressure could impact biomass accumulation. However, the Ecosim simulations do not address the spatial patterns of biomass accumulation. To explore how species and the fishery may move in

relation to retreating sea-ice, spatially and temporally dynamic simulations can be created in Ecospace (Steenbeek et al. 2013).

The objective of this study is to create a temporally and spatially dynamic Ecospace model of the WAP and develop sea-ice and fishing level scenarios that explore spatial and temporal impacts of changing conditions. Once the Ecospace simulation is performing adequately, it and the previously calibrated (Chapter 2) Ecosim simulations will be used to explore potential impacts of future sea-ice loss and increasing fishing pressure in the region. These simulations will establish a baseline that marine protected area scenarios (Chapter 4) can be compared against.

Methods

Study Area

Statistical Subarea 48.1, in the southwest Atlantic, includes the waters of the Western Antarctic Peninsula and the South Shetland Islands. Statistical Subarea 48.1 was spatially simplified and represented as a grid within the Ecospace model. The model has a grid cell resolution of 100 km² and contains approximately 6,103 active cells (Figure 10). Active cells are cells where the depth is greater than 0 m, and are accessible to plankton and nekton. The cell resolution was selected to facilitate comparisons with spatial modeling efforts currently underway in the CCAMLR (Second WS-MPA Domain 1 2015).

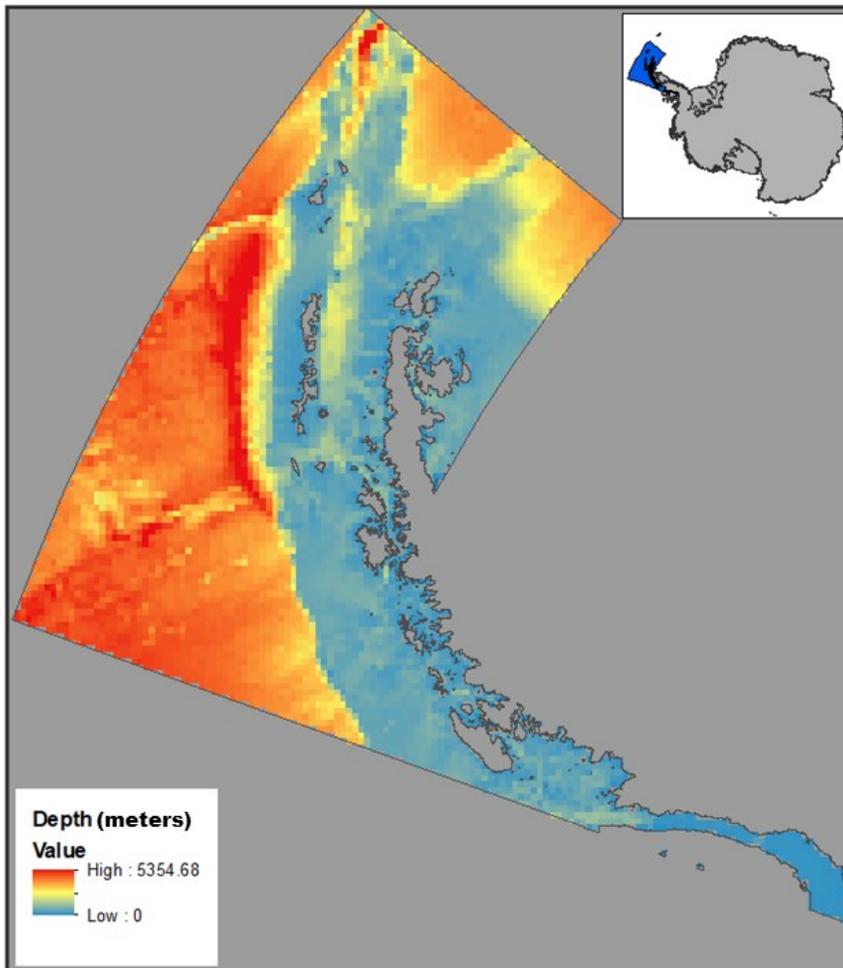


Figure 10. Ecospace study area. Inset map shows the location of the study area relative to the rest of the Antarctic continent. Bathymetry data (in meters) were accessed through the Marine Geoscience Data System (Carbotte et al. 2007). Areas that are shown in grey are inactive cells or were excluded from the study area and Ecospace model.

Ecosystem Model

Ecospace simulations use the food web (Ecopath) and time dynamic (Ecosim) simulations, as presented in Chapter 2, while adding spatial information regarding species distribution patterns and environmental drivers. The model includes 35 groups that were selected to represent the food web from plankton to apex predators. The eight species for

which monitoring data were available (Antarctic fur seals, Adélie penguins, chinstrap penguins, Gentoo penguins, *C. gunnari*, *G. gibberifrons*, *N. rossii*, and Antarctic krill) were modeled as single species groups. Ecosim simulations illustrated the importance of the sea-ice regime in determining patterns of biomass accumulation patterns for several species. The model was only able to recreate observed trends of abundance when the sea-ice regime was used to influence predator prey interactions. Ecosim simulations explore temporal dynamics only and are unable to capture the dynamic spatial component of the sea-ice regime. Local differences in timing of sea-ice formation and sea-ice extent can influence ecosystem-wide patterns (Ducklow et al. 2007, Ducklow et al. 2013). Recent improvements to the Ecospace module (Steenbeek et al. 2013) have allowed users to incorporate spatially and temporally explicit environmental drivers into the model.

The Ecospace scenario was tuned for the years 1996-2012, the same years for which times series data were available to fit the underlying Ecosim simulations (Chapter 2). While it is not possible to spatially fit the model, it is possible to judge if an Ecospace scenario is performing adequately by comparing it to what are known to be general patterns in species distribution and abundance patterns during the same period.

Input Maps

The basemap is composed of two maps, study area/excluded cells and bathymetry. The study area map was defined using the official CCAMLR shapefile detailing the geolocation of all Statistical Areas and Subareas (available from: <http://gis.CCAMLR.org/home>). Cells whose centers were outside of the CCAMLR boundary for Statistical Subarea 48.1, were excluded from the study area. The

bathymetry layer was defined using Antarctic bathymetry data (Carbotte et al. 2007) accessed through the Marine Geoscience Data System (<http://www.marine-geo.org>).

Primary production is also included as a static layer. The map for primary production was defined using chlorophyll *a* concentration in mg/m³ accessed through the Giovanni online data system (Acker and Leptoukh 2007). Data were available from SeaWifs missions for the years 1997-2010 and MODIS missions for the years 2010-2012. No data were available for the winter months, May-July. All available data were averaged by cell to create a mean primary productivity map.

In Ecospace, habitat capacity maps can be used to describe all potential foraging areas for each modeled group (Christensen et al. 2014). Habitat capacity allows the model to calculate foraging capacity by using spatial forcing functions³ 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 data poor response curves, maps derived from distribution maps based on sightings data and known foraging locations were used as a proxy 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 assigned a value between zero and one to distinguish the quality of the habitat. Ecospace does not recognize true zero, and so cells entered as zero could 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 are known 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 **Error! Reference source not found.** To facilitate comparison with the CCAMLR MPA planning efforts, every effort was made to utilize the same input data as the CCAMLR process. The process for creating the foraging area maps for each species is described below.

Table 6. Sources for foraging area maps.

Group #	Name	Foraging Area Map Source
1	Killer whales	Pers. Comm., Bob Pitman NOAA-AMLR, March 2015, Second WS-MPA Domain 1 (2015)
2	Leopard Seal	Pers. Comm., Doug Krause, NOAA-AMLR, March 2015, Burns et al. (2004), Burns et al. (2008), Forcada et al. (2012), Friedlaender et al. (2011), Meade et al. (2015)
3	Weddell Seal	Pers. Comm., Doug Krause, NOAA-AMLR, March 2015, Burns et al. (2004), Burns et al. (2008), Forcada et al. (2012), Friedlaender et al. (2011), Meade et al. (2015)
4	Crabeater Seal	Pers. Comm., Doug Krause, NOAA-AMLR, March 2015, Burns et al. (2004), Burns et al. (2008), Forcada et al. (2012), Friedlaender et al. (2011), Meade et al. (2015)
5	Antarctic fur seals	Pers. Comm., Mike Goebel and Doug Krause, NOAA-AMLR, March 2015, Second WS-MPA Domain 1 (2015)
6	S Elephant Seals	Costa et al. (2010), Hückstädt et al. (2012), Second WS-MPA Domain 1 (2015)
7	Sperm Whales	Whitehead (2003), Carbotte et al. (2007), Taylor et al. (2008)
8	Blue Whales	Kemp and Bennett (1932)
9	Fin Whales	Pers. Comm Christian Reiss and Jarrod Santorra, March 2015
10	Minke Whales	Second WS-MPA Domain 1 (2015), Friedlaender et al. (In Review)
11	Humpback whales	Friedlaender et al. (In Review), Second WS-MPA Domain 1 (2015)
12	Emperor Penguins	Kirkwood and Robertson (1997), Wienecke and Robertson (1997), Second WS-MPA Domain 1 (2015)
13	Gentoo Penguins	Pers. Comm., Jefferson Hinke, NOAA-AMLR, March 2015, Second WS-MPA Domain 1 (2015)

14	Chinstrap Penguins	Pers. Comm., Jefferson Hinke, NOAA-AMLR, March 2015, Hinke et al. (2015), Second WS-MPA Domain 1 (2015)
15	Adélie Penguins	Jefferson Hinke, Pers. Comm. March 2015, Hinke et al. (2015), Erdmann et al. (2011) Second WS-MPA Domain 1 (2015)
16	Macaroni Penguins	Green et al. (2005), (Bost et al. 2009), Naveen and Lynch (2011)
17	Flying Birds	This species group is large and diverse, the foraging area was not constrained in the model
18	Cephalopods	This species group is large and diverse, the foraging area was not constrained in the model
19	Myctophids (Off shelf)	Hill et al. (2007) defined off-shelf waters as deeper than 500m
20	On-shelf fish	Hill et al. (2007) defined shelf waters as shallower than 500m
21	<i>N. rossii</i>	DeWitt et al. (1990)
22	<i>C. gunnari</i>	Iwami and Kock (1990) Kock and Jones (2005)
23	<i>G. gibberifrons</i>	Iwami and Kock (1990) Kock and Jones (2005)
24	Salps	Pers. Comm., Christian Reiss, NOAA-AMLR, March 2015, Second WS-MPA Domain 1 (2015)
25	Benthic Invertebrates	Lockhart and Jones (2008), Gutt et al. (2013)
26	Large Krill	Second WS-MPA Domain 1 (2015)
27	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)
28	Other Euphausiids	Fisher et al. (2004) Pers. Comm., Christian Reiss, NOAA-AMLR, March 2015, (Second WS-MPA Domain 1 2015)
29	Microzooplankton	This species group is large and diverse, the foraging area was not constrained in the model
30	Mesozooplankton	This species group is large and diverse, the foraging area was not constrained in the model
31	Macrozooplankton	This species group is large and diverse, the foraging area was not constrained in the model
32	Small phytoplankton	This species group is large and diverse, the foraging area was not constrained in the model
33	Large Phytoplankton	This species group is large and diverse, the foraging area was not constrained in the model
34	Ice Algae	Cavalieri et al. (1996, updated yearly)
35	Detritus	

Foraging area maps for cetaceans were created using historic whaling data or by drawing convex hulls around areas where animals were sighted or tracked (

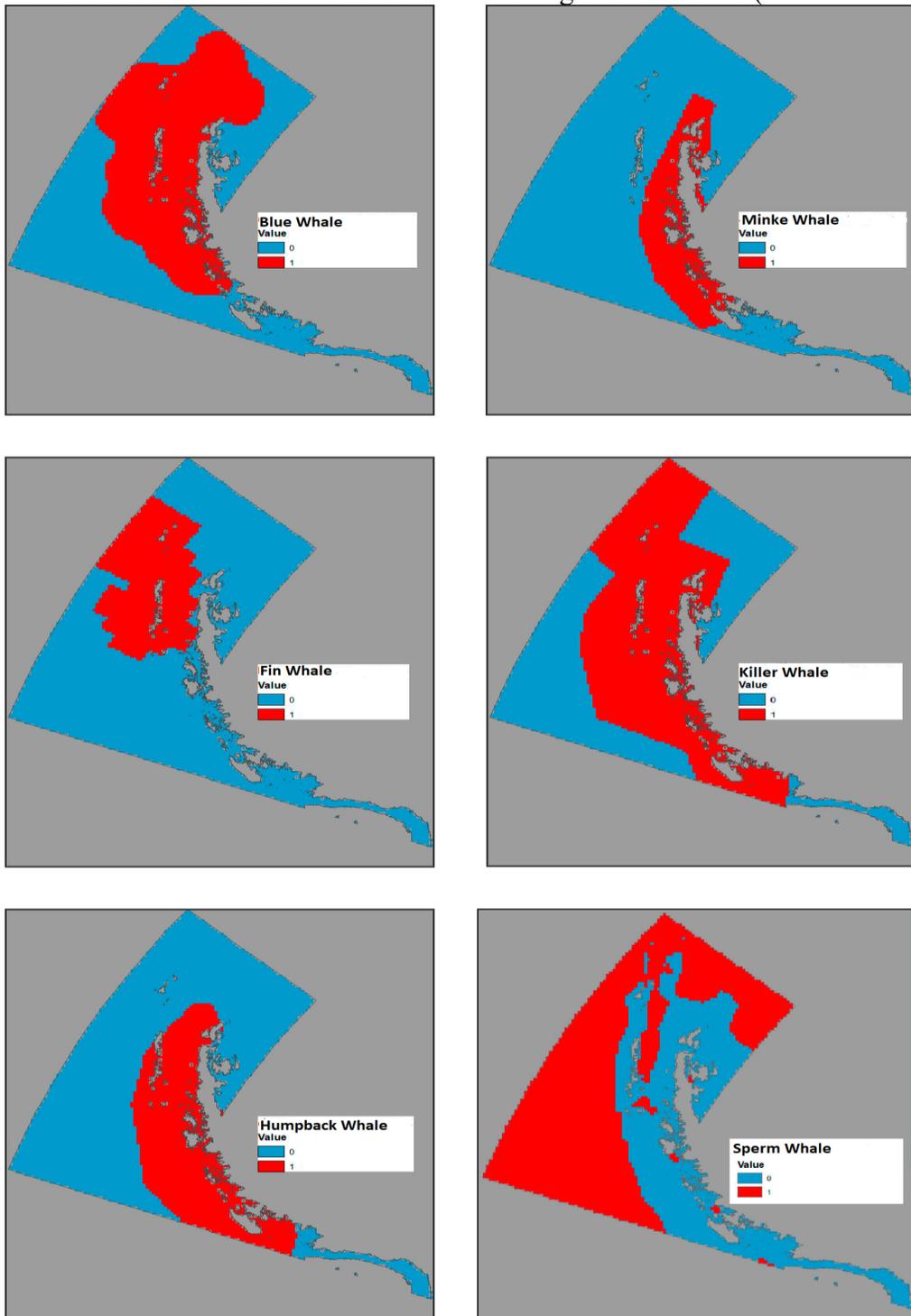


Figure 11). Only historic whaling data were available for blue whales and the map was created solely from these data (Kemp and Bennett 1932). Both historic whaling data

(Kemp and Bennett 1932)) and modern sighting data (Pers. Comm. Christian Reiss and Jarrod Santora, March 2015) were available for fins whales. The two datasets had a high degree of overlap in the central region where historic catches were highest and modern sightings occurred. The fishery-independent modern sightings data were used to draw the map. Only satellite tracking data were available to inform the foraging area maps for humpback and minke whales (Second WS-MPA Domain 1 2015, Friedlaender et al. In Review). No regionally specific sighting or tacking data were available for sperm whales. Sperm whales (*Physeter macrocephalus*) prefer to forage in waters deeper than 1000 m (Whitehead 2003, Taylor et al. 2008). The sperm whale foraging area map was restricted

to waters deeper than 1000 m (

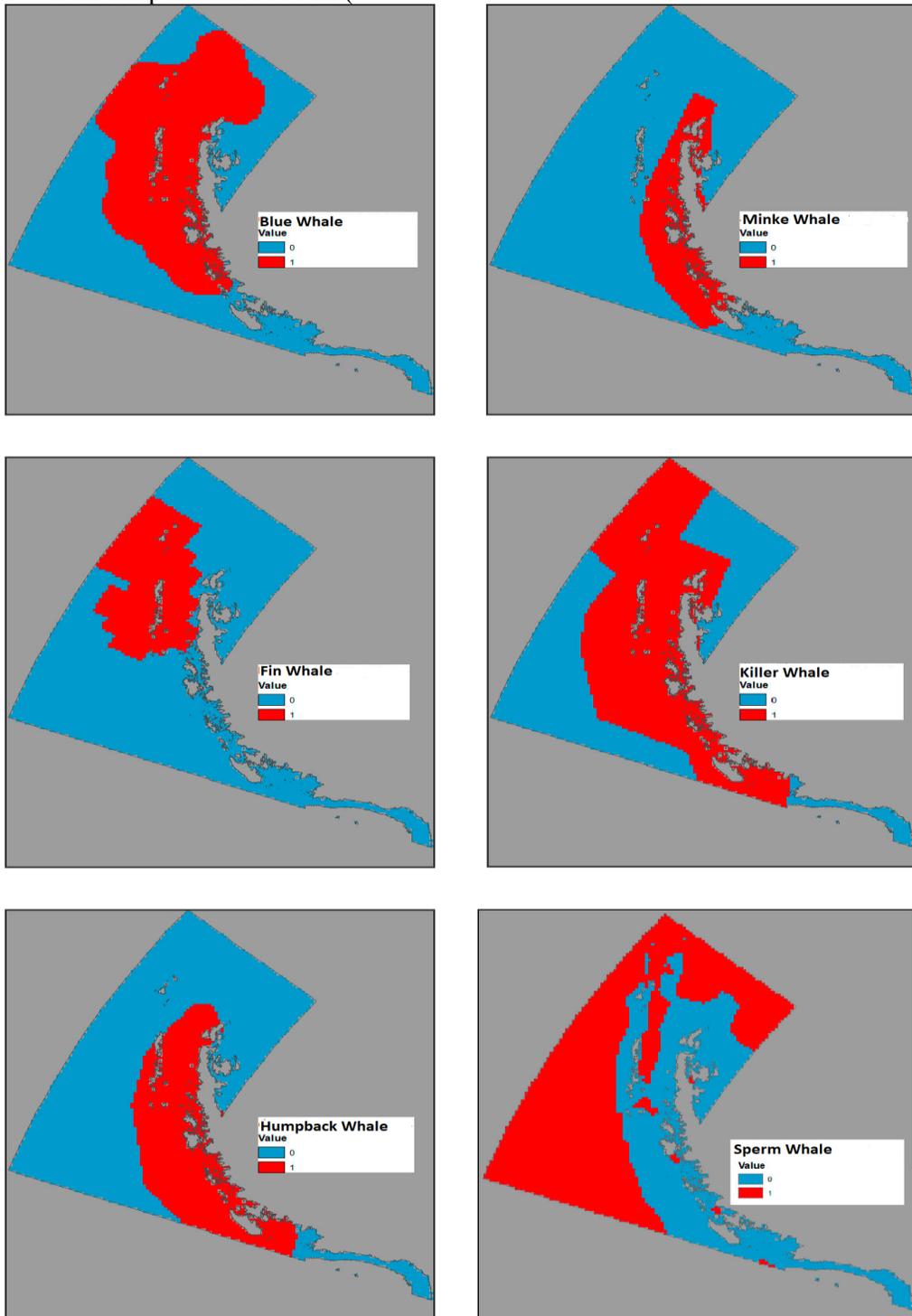


Figure 11.) and depth data were accessed through the Marine Geoscience Data System (Carbotte et al. 2007). Because of low sample size, and in some cases the historic

nature of the data, areas were either classed as potential foraging areas (value of 1) or not (value of zero) for all modeled cetacean species.

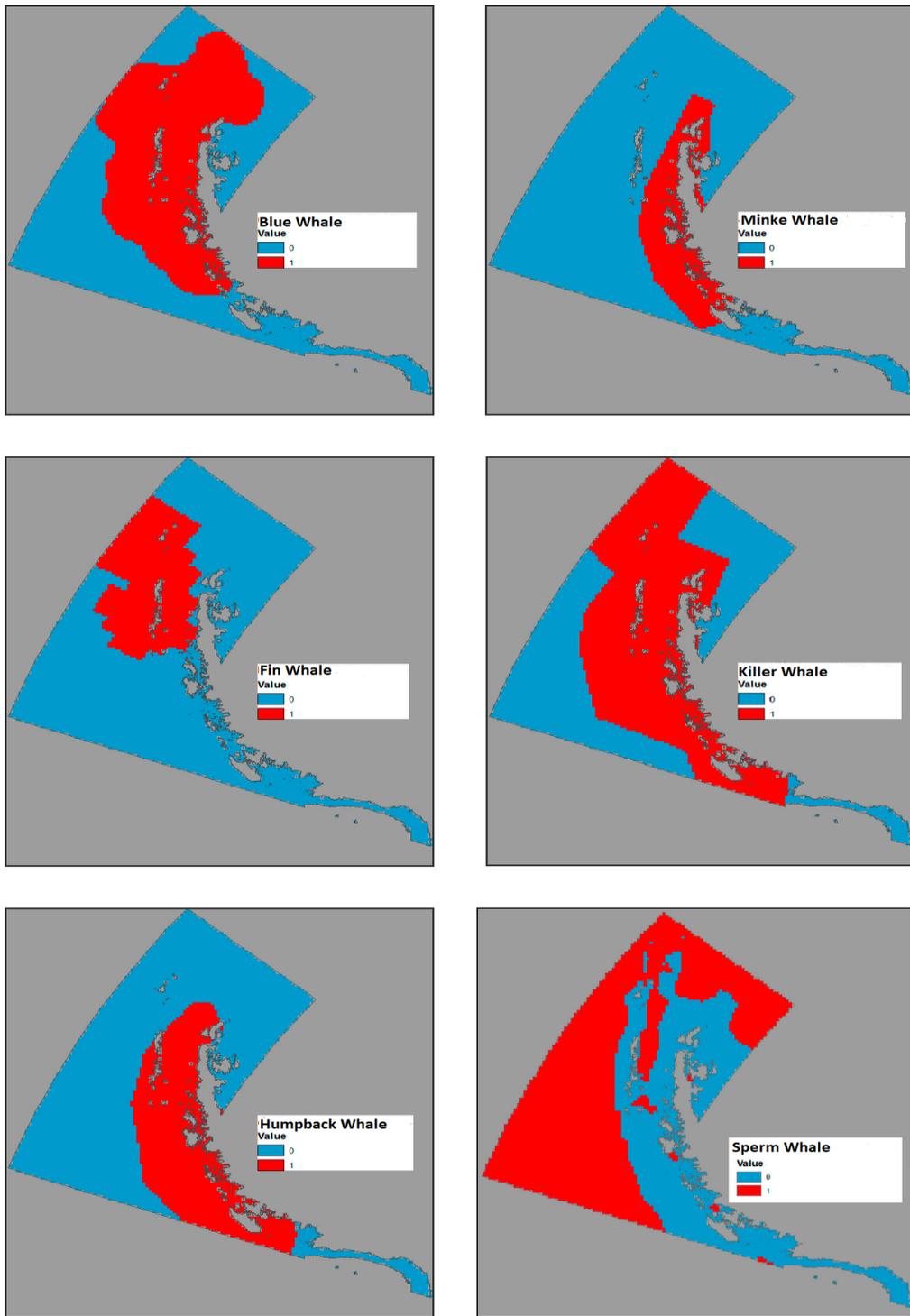


Figure 11. Cetacean foraging areas.

Some tracking and sighting data are available for ice seals (Weddell seals, *Leptonychotes weddellii*; Leopard seals, *Hydrurga leptonyx*; and Crabeater seals, *Lobodon carcinophagus*). These seals are known to be dependent on the pack ice environment and to co-occur (Burns et al. 2004, Burns et al. 2008, Friedlaender et al. 2011, Forcada et al. 2012, Meade et al. 2015), but the sighting and tracking data for each species are sparse. The same foraging area map was used for all three ice seal species (Figure 12). It was drawn to include areas where any of the three species have been tracked or sighted (Burns et al. 2004, Burns et al. 2008, Friedlaender et al. 2011, Forcada et al. 2012, Meade et al. 2015) as well as connecting areas thought to be pack ice environment for at least part of the year (Second WS-MPA Domain 1 2015). All cells within the region where animals had been sighted or tracked and the connecting pack ice environment were assigned a value of 1, all other areas were assigned a zero value (Figure 12).

The foraging area map for Antarctic fur seals (*Arctocephalus gazella*) was drawn around winter tracking data (Second WS-MPA Domain 1 2015) and around a 75 km foraging buffer associated with colonies surveyed by NOAA-AMLR (Goebel and Reiss 2014). Recognizing that 85% of the fur seal population in the region produces pups at Cape Shirreff (Hucke-Gaete et al. 2004, Schwarz et al. 2013, Goebel and Reiss 2014), the foraging buffer around Cape Shirreff was rated as the highest quality habitat and assigned a value of 1. Areas contained within other colony foraging buffers were assigned an intermediate value of 0.75, and areas only accessed during the winter or by non-breeding individuals in the summer were assigned a value of 0.5 (Figure 12).

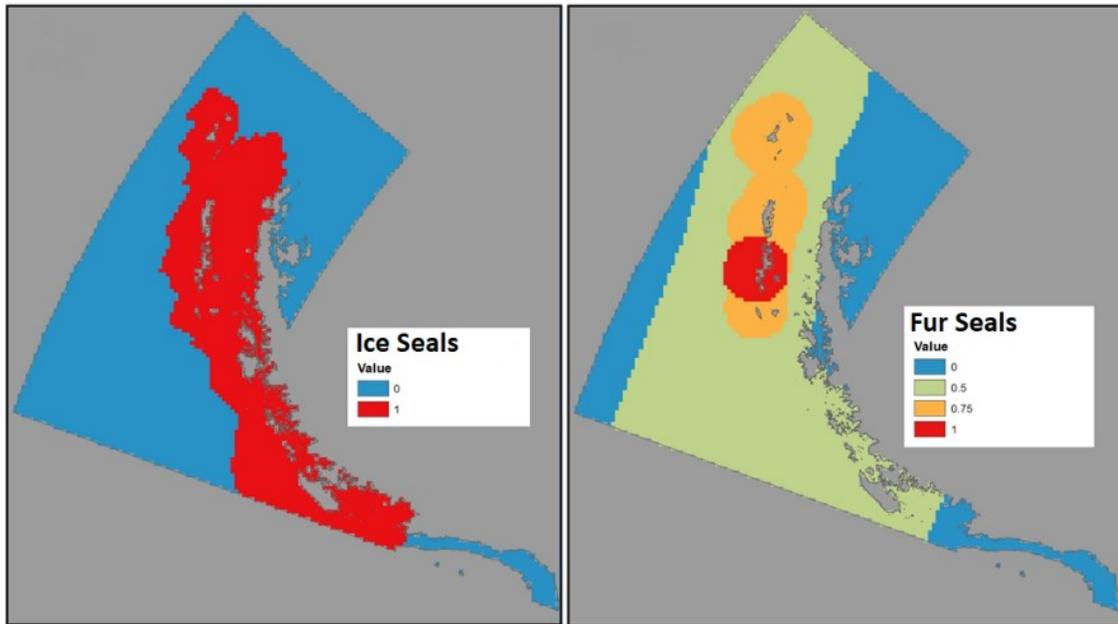


Figure 12. Foraging areas for seals.

Penguin foraging area maps were drawn around areas shown to be utilized by tracked penguins and areas within the foraging buffer of known penguin colonies. Emperor penguins (*Aptenodytes forsteri*) are known to travel 120 km away from their colonies and seek out waters shallower than 500 m in which to forage (Kirkwood and Robertson 1997, Wienecke and Robertson 1997). A 120 km buffer was established around the two known emperor colonies in the region (Trathan et al. 2011 and see Figure 13). Macaroni penguins (*Eudyptes chrysolophus*) are known to range widely while foraging, particularly in the winter. They have been tracked moving as far as 572 km from their colonies during winter foraging trips (Green et al. 2005, Bost et al. 2009). A larger buffer towards northern ice free areas (Figure 13) was added to the location of

known Macaroni penguin colonies (Naveen and Lynch 2011). These buffers are consistent with those used in the CCAMLR Process (Second WS-MPA Domain 1 2015).

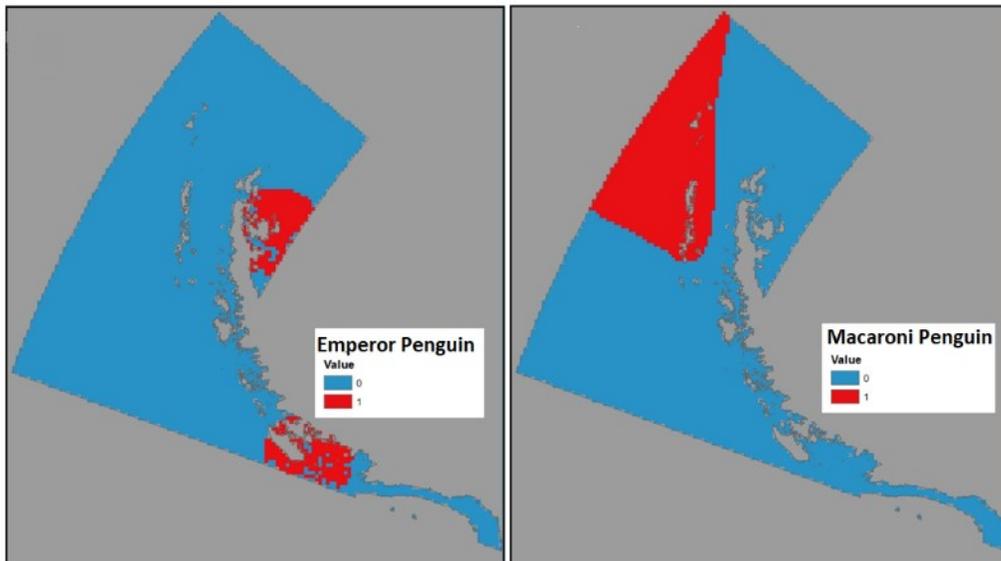


Figure 13. Foraging areas for Emperor and Macaroni Penguins.

Foraging area maps for the three pygoscelid penguins were graded to reflect the greater concentration of animals near the colonies during the summer. Adélie (*Pygoscelis adeliae*), Chinstrap (*Pygoscelis antarcticus*) and Gentoo (*Pygoscelis papua*) penguin colonies were encircled by 25 km foraging buffers (Second WS-MPA Domain 1 2015 and Figure 14). Adélie penguins living in the South Shetland islands are known to avoid waters on the northwest side of the islands (Hinke et al. 2017), so buffers for these colonies were truncated. Areas contained within the colony foraging buffers were assigned a value of 1. Winter foraging areas were drawn to encompass areas used by

satellite tagged birds (Second WS-MPA Domain 1 2015 and Figure 14) and were assigned a value of 0.3.

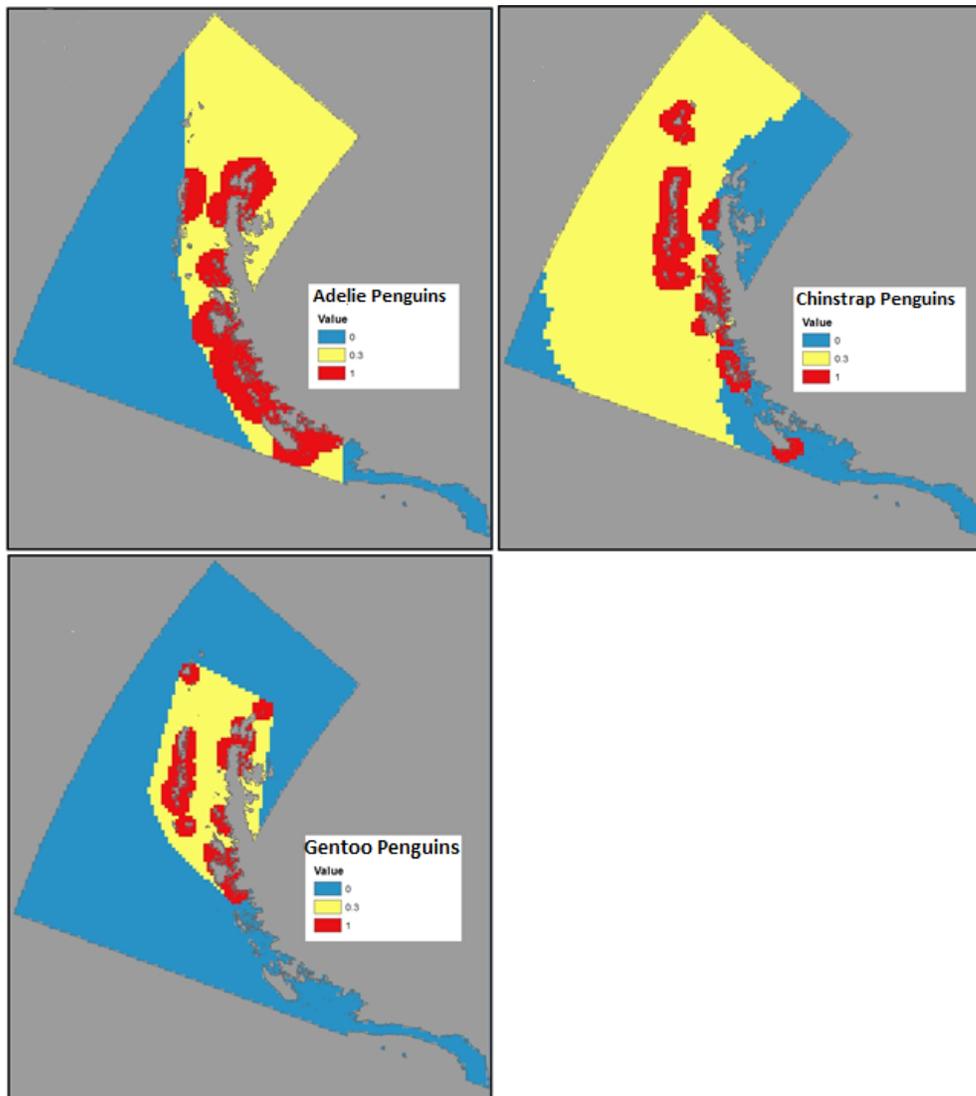


Figure 14. Foraging areas for Adélie, Chinstrap, and Gentoo Penguins.

The fish species included in the model can generally be described as off-shelf (Myctophids) or on-shelf (all other modeled fish species and groups). Hill et al. (2007)

define the continental shelf break for Statistical Subarea 48.1 to occur at 500 m depth. The functional group “On-shelf fish” was assigned to areas shallower than 500 m, where depth data were accessed through the Marine Geoscience Data System (Carbotte et al. 2007). The foraging areas of the three on-shelf species of fishes modeled as single species functional groups were further constrained by published range maps (DeWitt et al. 1990, Iwami and Kock 1990 and Figure 15). *C. gunnari*, *G. gibberifrons* and *N. rossii* have not been found southwest of Anvers island (DeWitt et al. 1990, Iwami and Kock 1990), and the input maps reflect this. Myctophids were assigned to habitat deeper than 500 m. Foraging area maps for all modeled fish groups (Figure 15) were classified as either foraging areas (value of 1) or not foraging areas (value of 0).

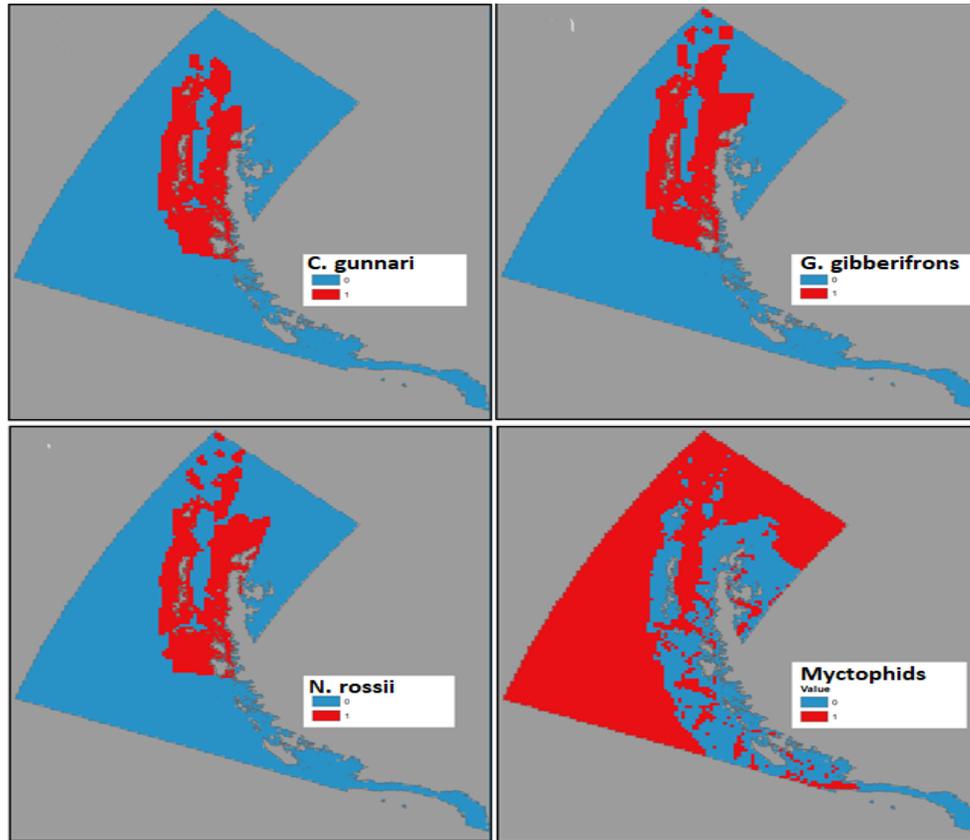


Figure 15. Foraging areas for fish.

No comprehensive benthic invertebrate abundance or density data for the region could be found in the literature. Gutt et al. (2013) collated the existing benthic invertebrate data for the region and this compilation indicated that biomass is concentrated in waters shallower than 800 m. Lockhart and Jones (2008) found that shallow waters where the temperature is colder than 1°C, had higher biomass than warmer, deeper waters. A climatology describing sea floor temperature from 1955-2012 presented in a 0.25 latitudinal degree grid was accessed from the World Ocean Atlas (Boyer et al. 2013). The raster was reclassified into two classes. One class had a bottom temperature less than 1°C and the second class had a bottom temperature greater than

1°C. Similarly, the bathymetry raster, accessed through the Marine Geoscience Data System (Carbotte et al. 2007), was reclassified into areas shallower and deeper than 800 m. In Arc Map, select by location was used to identify grid cells in the frame that overlapped with regions shallower than 800 m and areas colder than 1°C. These cells were assigned a value of 1. Cells identified as overlapping with shallow areas warmer than 1°C were assigned a value of 0.66. All other cells were assigned a value of 0.33 (Figure 16).

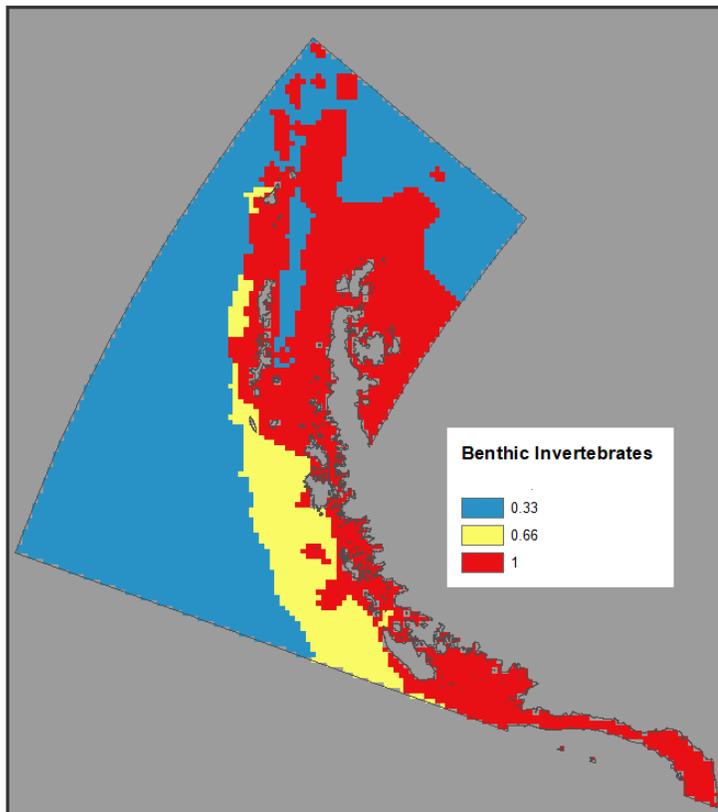


Figure 16. Foraging areas for benthic invertebrates.

Foraging area maps for krill, salps and other euphausiids were developed from interpolated density rasters derived from multi-year biomass data sets collected by

several research groups (Second WS-MPA Domain 1 2015). The foraging area map for small krill was additionally informed by locations of suspected krill nurseries (Huntley and Brinton 1991, Frazer et al. 2002, Pakhomov et al. 2004, Ashjian et al. 2008, Siegel et al. 2013). The foraging area map for other euphausiids was additionally informed by large catches of *Thysanoessa macrura* reported in the Western Weddell Sea (Fisher et al. 2004). To create the maps for Ecospace (Figure 17), the zooplankton density maps were resampled to 10 km x 10 km, using bilinear resampling and the 10 km x 10 km fishnet frame as a snap raster. The resampled rasters were then classified into three quantiles based on density. The top third densest areas were assigned a value of 1, the middle third 0.75 and the bottom third 0.25. Areas not sampled were given a default value of 0.25

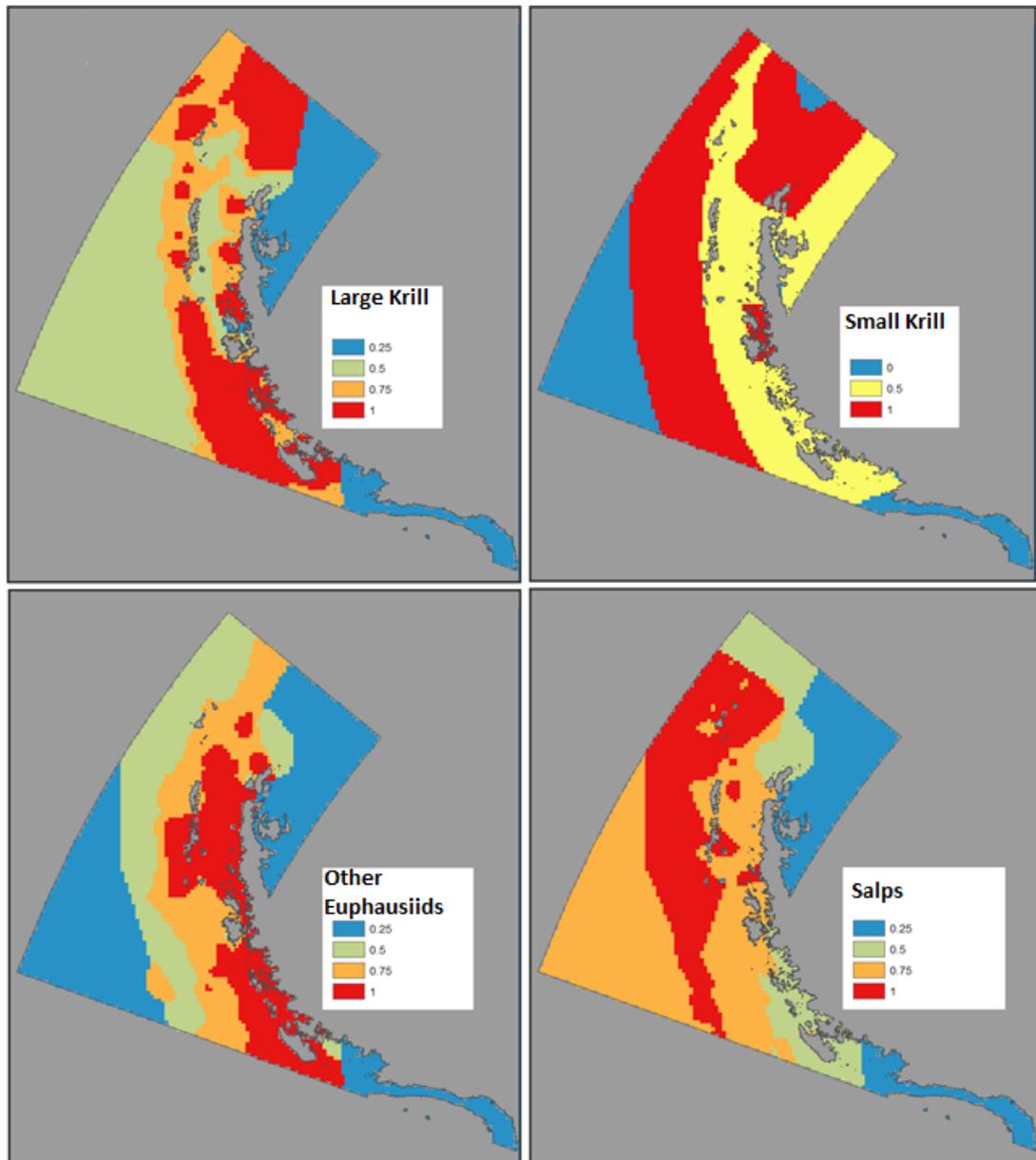


Figure 17. Foraging areas for Large Krill, Small Krill, Other Euphausiids, and Salps.

All other zooplankton and flying bird foraging area maps were set to a uniform value of one throughout the study region. These model groups are large multispecies assemblages and may range throughout the study area. Recent work on at sea seabird sightings data indicates that there are oceanic hotspots for seabirds in the Western

Antarctic Peninsula region (Santora et al. 2017). However, the sampling area for those surveys was not sufficiently large to be representative of the entire Statistical Subarea 48.1 and seabird hotspots were not used to inform the Ecospace simulations.

Dispersal

Biomass dispersal speed, whether through active swimming or drifting with the current, can influence spatial patterns of biomass accumulation. In general, animals that swim quickly are more likely to swim out of any given cell between time steps, than animals that swim more slowly. In Ecospace, movement rates across planning unit boundaries are related to annual movement distances (Walters et al. 1999, Martell et al. 2005). Movement rates, M_i , were calculated from swim speeds to estimate the proportion of biomass exiting any given planning unit, 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.

$$M_i = \frac{S_i}{\pi L} \quad \text{Equation 7}$$

S_i is the swim speed (or current speed for plankton) and L is the length of the side of the planning units (10 km). The source for swim speeds and base dispersal rates entered into the model are shown in Table 7. Dispersal speed.

In Ecospace, dispersal speed varies across groups and 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 as more suitable by the habitat capacity module or, in the case of this model, cells with higher values in the input foraging areas maps.

Table 7. Dispersal speed.

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	Bengtson et al. (1993), Nordøy et al. (1995), Adam (2005)	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
Gentoo 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

Sea-ice Forcing

Using foraging areas maps in the habitat capacity module somewhat limited the area accessible to each species or functional group. Ecospace does not recognize true zero cell values, so cells assigned a value of zero in the input map could increase in importance as environmental conditions change within the simulation. Inclusion of forcing functions and associated responses curves worked to move species within their suitable habitat, as defined by the foraging area maps. Spatially and temporally dynamic forcing functions were used to influence patterns of biomass accumulation, and to shift species patterns of concentration at each time step in response to changing environmental conditions. It is possible that cells assigned zero value at input could experience increasing importance as environmental conditions changed within the simulation.

The spatio-temporal framework (Steenbeek et al. 2013) was used to include monthly maps of sea-ice concentration and its inverse, open water concentration. Monthly averages of sea-ice concentration were accessed through the National Snow and Ice Data Center for the years 1996-2012 (Cavalieri et al. 1996, updated yearly). Data are presented as a percentage of 100 (Figure 18). The inverse open water maps were created by subtracting the grid cell specific sea-ice concentration from 100 (Figure 18). Paired maps were created for every month simulated.

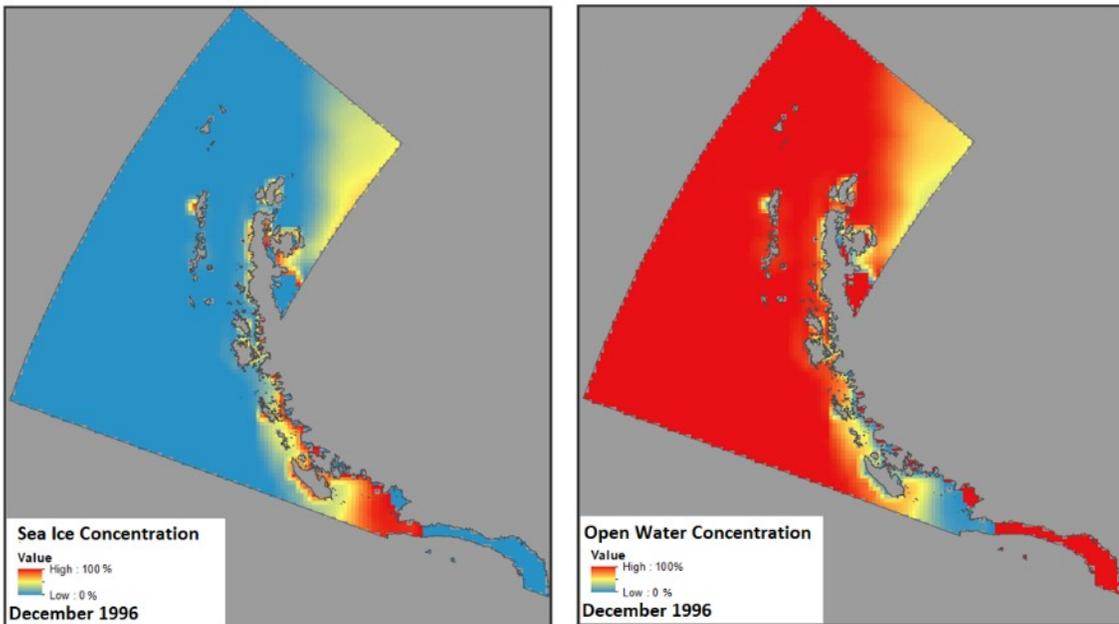


Figure 18. Example of paired sea-ice and open water maps. Paired maps were created for every month simulated.

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 sighting data and reported trends in abundance as reference. Seven groups were assigned a positive response to sea-ice. Antarctic fur seals experience less Leopard seal predation in icier conditions (Goebel and Reiss 2014), so they were assigned a positive response to increasing sea-ice. Existing literature and Ecosim simulations (Chapter 2) indicate that Adélie penguins (Trivelpiece et al. 2011, Lynch et al. 2012, Hinke et al. 2014), Chinstrap penguins (Trivelpiece et al. 2011, Lynch et al. 2012), and krill (Atkinson et al. 2004, Atkinson et al. 2009) have increased abundances associated with periods of icier conditions. Ecosim simulations (Chapter 2) indicate that

G. gibberifrons biomass responds positively to increasing sea-ice, which may be driving the significant decline documented in field observations (Kock and Jones 2012). The last group assigned a positive response to sea-ice concentration is ice algae, as the definition of that group is algae living in sea-ice. Eight groups were assigned a positive response to open water. Tracking data of humpback whales indicates that they prefer ice edge and open water environments (Friedlaender et al. 2011, Friedlaender et al. In Review). Sperm whales prefer to forage in deep, ice free waters (Taylor et al. 2008). Gentoo penguins (Forcada et al. 2006, Hinke et al. 2007) and salps (Atkinson et al. 2004) exhibit increased abundance with increasing open water conditions. Macaroni penguins have been expanding their range and moving further south as ice recedes (Gorman et al. 2010) and travel great distances from their colonies in winter to access open water areas (Green et al. 2005, Bost et al. 2009). *C. gunnari* (Iwami and Kock 1990) and *N. rossii* (DeWitt et al. 1990) prefer ice-free waters. The species comprising the other euphausiids functional group, *Thysanoessa macrura* and *Euphausia crystallorophias*, are found in greater densities in ice free areas (Fisher et al. 2004, Second WS-MPA Domain 1 2015).

While several response curves were tested, ultimately only variations of a linear response were retained in the model. Two linear curves were retained in the model to describe species' response to sea-ice concentration; a steeper curve was applied to animal species and a more gradual slope was applied to ice algae (Figure 19). Three linear response curves of different slope were applied to describe species' response to open water (Figure 20). A steeper curve was applied to *C. gunnari* and Gentoo penguins to get Ecospace to be consistent with field observations by indicating biomass increases for

these species (Kock and Jones 2012, Lynch et al. 2012). A very shallow curve was applied to salps to allow the model to indicate a moderate increase in salp biomass in accordance with the literature (Atkinson et al. 2004). A slightly steeper curve was applied to the remaining species that respond positively to open water (Figure 20) so that Ecospace simulation outcomes would indicate a moderate increase in biomass. Curves were selected and retained based on impact on spatial distribution and relative biomass outcomes for the species the curve was applied to. Two examples of fitting curves are described below. Similar procedures were used to decide curves for all 15 of the model groups that were assigned a response to either sea-ice concentration or open water concentration.

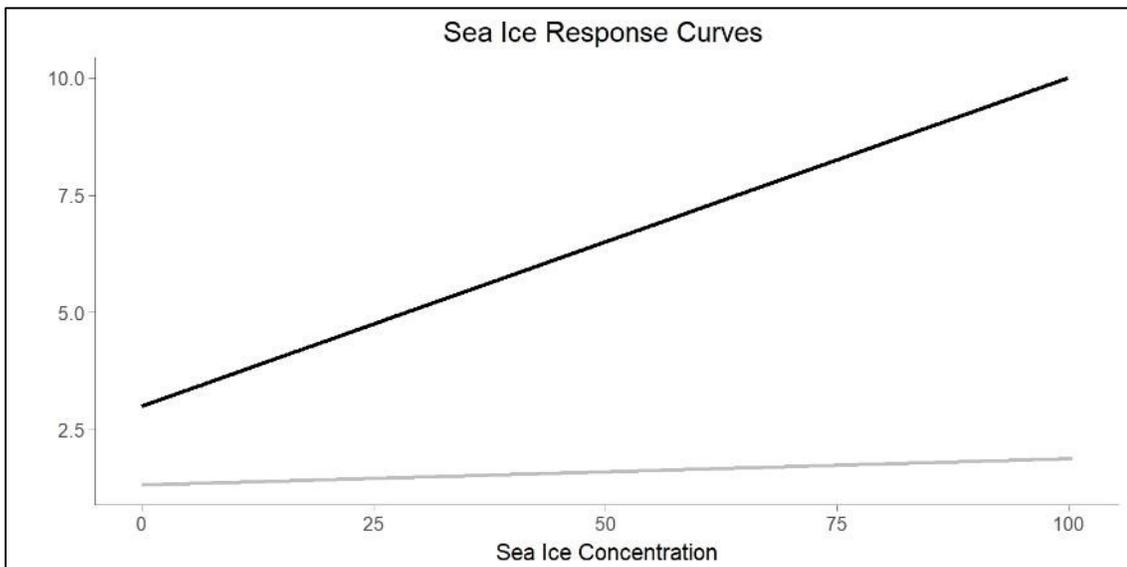


Figure 19. Spatial Sea-ice response curves. The steeper curve (black) was applied to fur seals, Chinstrap penguins, Adélie penguins, *G. gibberifrons*, Large Krill and small krill. The more gradual curve (grey) was applied to ice algae.

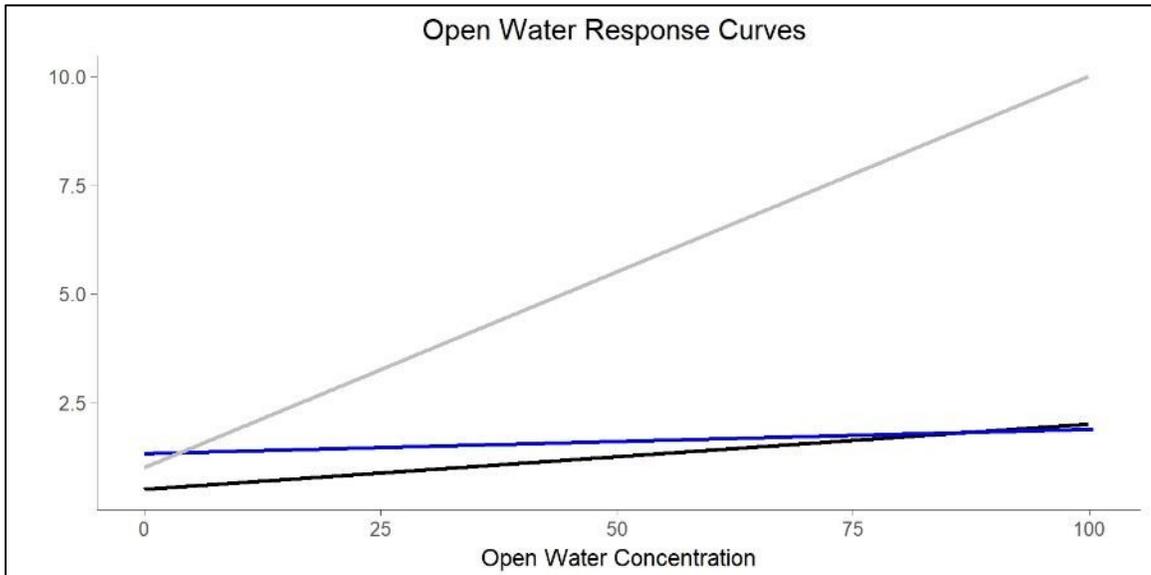


Figure 20. Spatial open water response curves. The steeper curve (grey) was applied to Gentoo penguins and *C. gunnari*. The very shallow curve (blue) was applied to salps. The black curve was applied to Sperm Whales, Humpback Whales, Macaroni penguins, *N. rossii* and Other Euphausiids

Adélie penguin populations respond to changes in sea-ice conditions (Croxall et al. 2002, Jenouvrier et al. 2005, Hinke et al. 2014) and prefer foraging 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 (Figure 21 A). In the first, Adélie penguins responded positively when there was greater than 15% sea-ice concentration, and had no response to lower ice concentrations. This is effectively an on/off switch that informs the model that Adélie penguins will not occupy cells that have little or no sea-ice. The use of this curve resulted in the elimination of Adélie penguins from their known colonies prior to 2012 (Figure 21 C). Adélie penguins have high site fidelity (Trivelpiece et al. 1987), and will return to their natal colonies regardless of local ice conditions. A

linear response to sea-ice, where Adélie penguins do better with increasing ice concentration 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 (Figure 21 D). This result mimics what has been observed in the region (Lynch et al. 2012). The linear response curve was retained in the model.

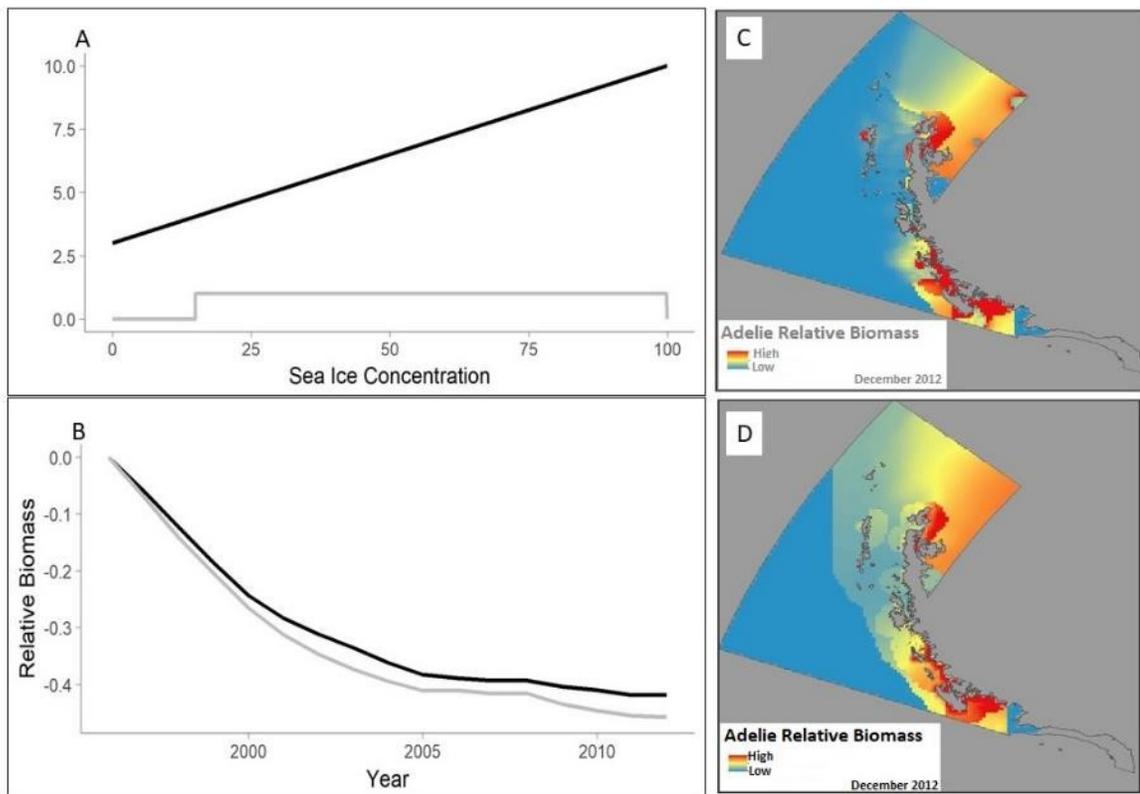


Figure 21. Spatial response curves tested for Adélie Penguins. Two curves describing Adélie penguin response to sea-ice concentration were tested in Ecospace (A), a curve where there is no response until 15% concentration (grey), and a linear response (black) Regardless of the curve used, the temporal 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 non-linear 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 are still occupied (D).

Salps, specifically *Salpa thompsoni*, are an important open water pelagic zooplankton that is increasing in abundance and replacing krill in some regions (Atkinson et al. 2004, Atkinson et al. 2009). Initial implementation of the Ecospace simulation without using open water concentration as an environmental driver to force salp dynamics indicated the opposite pattern (Figure 22). To correct this, two linear positive responses to open water concentrations were attempted (Figure 23 A). While the slope of the line significantly impacted relative biomass simulation outcomes (Figure 23 B), there was very little difference in spatial distribution of salp relative biomass (Figure 23 C and D). Using the steep linear response resulted in significant growth in salp relative biomass and caused crashes in mesozooplankton. The shallower curve that yielded the more moderate relative biomass increase was retained in the model.

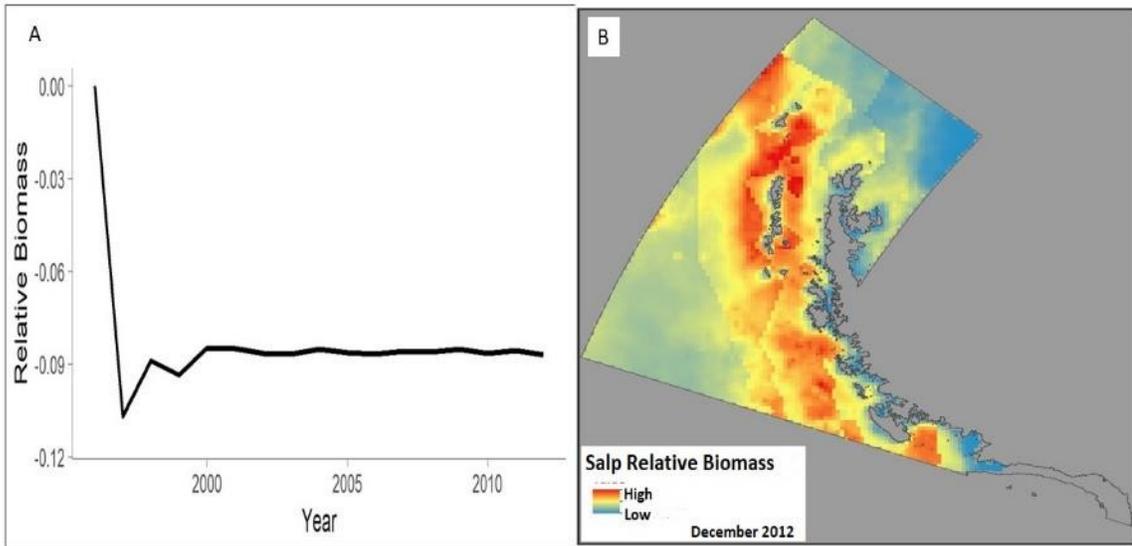


Figure 22 Simulation outcomes for salp biomass without sea-ice forcing. Ecospace simulations indicated a decline in Salp relative biomass (A), the opposite patterns describe by Atkinson et al. (2004). Note Figure 23 Below, that the spatial patterns of biomass accumulation (B) did not change significantly when forcing is applied.

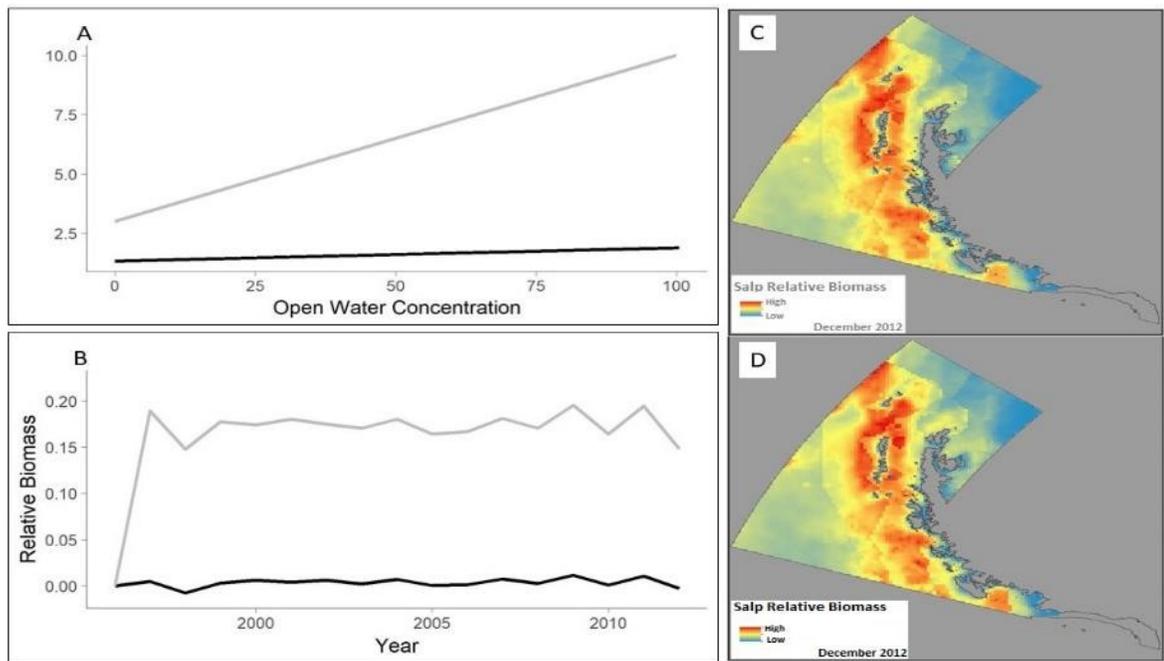


Figure 23. Spatial response curves tested for salps. Two curves were tested to describe salp response to open water (A). Relative log Biomass outcomes varied significantly between curves with the steeper (gray) curve resulting in much higher biomass outcomes (B), but spatial distribution patterns were similar (C and D). The shallower (black) curve was retained.

Recreating Spatio-Temporal Patterns in Fishing

Spatio-temporal dynamics of the fishery were included by using the spatial temporal framework to influence the “cost” associated with fishing in each grid cell. When cost information is input in the model, Ecospace causes the fleet to gravitate towards cells with the lowest assigned costs and away from higher cost cells (Christensen and Walters 2004). The CCAMLR subdivides Statistical Subarea 48.1 into eight Small Scale Management Units (SSMUs). Catch and hours fished in each SSMU are reported annually (CCAMLR 2017). These values were then associated with the CCAMLR provided shapefile of SSMU boundaries (<https://gis.CCAMLR.org/home>), to make monthly maps of catch per SSMU. Catch between SSMUs in each month was scaled such that the area with the highest catch had the lowest cost value. The scaling was performed for every month starting January 1996 and ending December 2012. The following equation was used to perform the scaling. Use of the 1.1 multiplier ensured that no SSMUs were assigned a value of 0.

$$Cost_{SSMU_i} = \frac{(Total\ Catch * 1.1) - catch\ in\ SSMU_i}{Total\ Catch * 1.1} \quad \text{Equation 8}$$

Where *Total Catch* is the catch across all SSMUs at any given time step and the 1.1 constant is simply a value that prevents a zero value from occurring. EwE does not accept zero cost values.

Months for which no fishing occurred and SSMUs in which no fishing occurred in a specific month were assigned a uniform value of 1000. These weighted cost maps effectively restricted the fishery to only operate in SSMUS where fishing occurred during each time step (Figure 24).

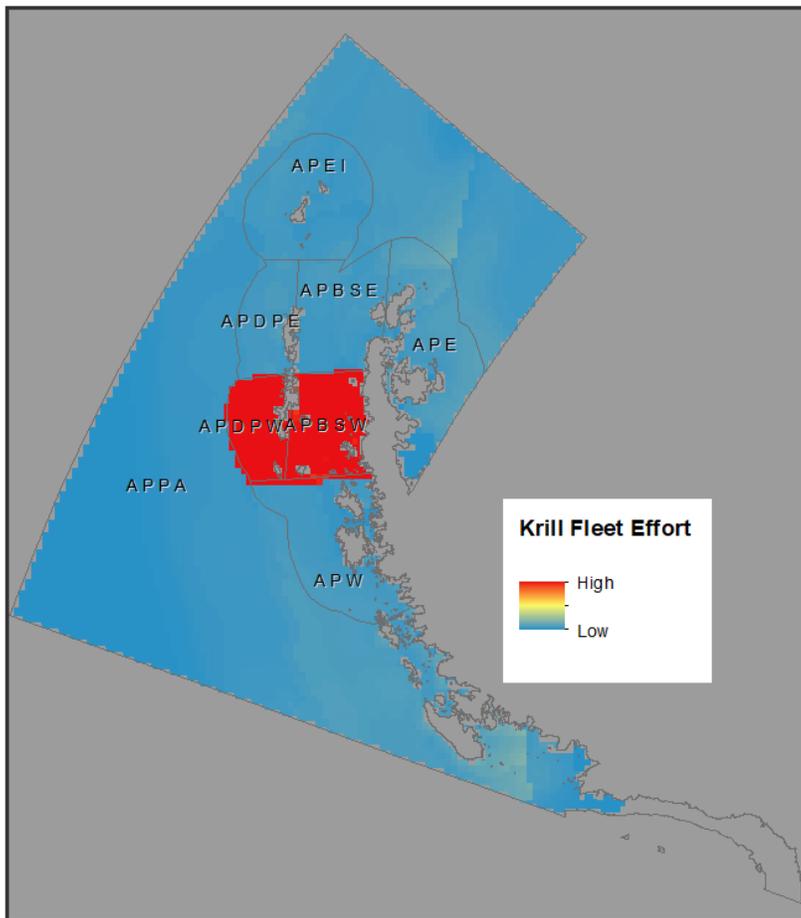


Figure 24. Example Ecospace recreation of reported fishing locations. Model output showing locations of fishing fleet effort in July of 1998. The eight SSMUs are 1- Antarctic Peninsula Pelagic Area (APPA); 2- Antarctic Peninsula West (APW); 3- Drakes Passage West (APDPW); 4- Drakes Passage East (APDPE); 5- Bransfield Strait East (APBSE); Elephant Island (APEI); Antarctic Peninsula East (APE). In reality, fishers only operated in two SSMUs APDPW and APBSW (CCAMLR 2017). By using the heavily weighted cost layers, the model adequately recreated monthly SSMU specific fishing patterns.

Sea-ice Scenarios

It is widely acknowledged that sea-ice conditions in the region drive ecosystem patterns, are rapidly changing, and that there is an expectation of decreased sea-ice in future years (Ducklow et al. 2007, Martinson et al. 2008, Vernet et al. 2008, Ducklow et al. 2013). However, currently no good spatially explicit predictions of sea-ice concentration are available. Therefore, a sensitivity analysis was conducted that used two possible sea-ice scenarios: one in which conditions stayed the same as they were from 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 (described in Chapter 2). Bins were defined using natural breaks in the data (Table 8).

Table 8 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. 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:

$$Bin = Truncation[4 * R^{f(t)}] \quad \text{Equation 9}$$

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 below (**Error! Reference source not found.**), 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.

A second equation (Equation 10) was used to determine the annual exponent in Equation 9. The output from Equation 10 is a value between 1 and 20 inclusive, and changes each year of the time series.

$$f(t) = 1 + (19 * \left(\frac{t}{100}\right)^3) \quad \text{Equation 10}$$

Where t is a year in the 100-year time series from 1 to 100. The constant value 1, ensures that the output of Equation 10 is greater than or equal to 1. Without this addition Equation 10 could produce a result less than one, which, when used as an exponent in Equation 9, 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.

Applying Equations 9 and 10 biased bin selection towards bin 0 as the year in the scenario increased to 100. The effectiveness of this biasing function was illustrated by examining the selection probability distribution at six discrete time steps in the 100-year series (Figure 25). The resulting sea-ice time series, and corresponding sea-ice indices for both the status quo scenario and decreasing sea-ice scenario are shown below (Figure 26).

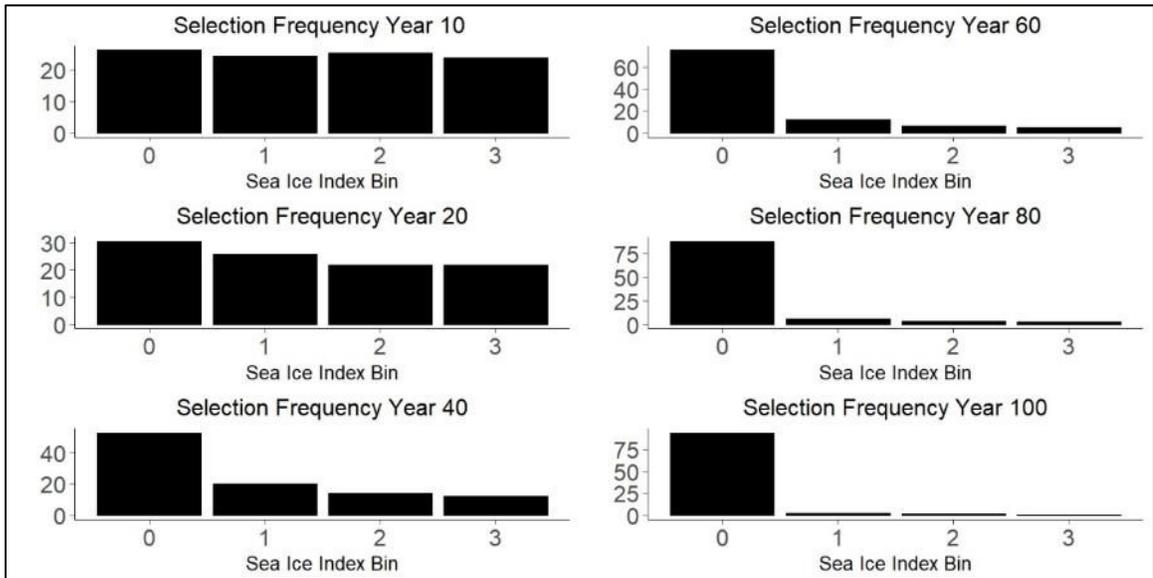


Figure 25. Selection distribution of sea-ice index bins. At each time step, 4,000 selections were performed. The bars represent the frequency that each sea-ice index bin was selected at the specified time step. The biasing function strongly favors the lowest ice index bin by about year 40.

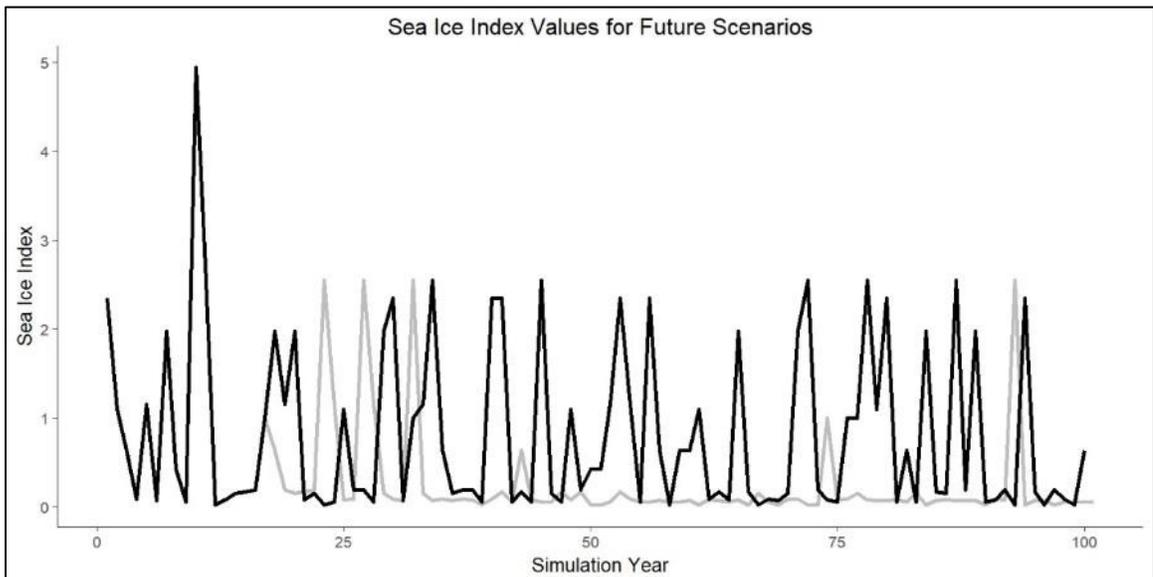


Figure 26. Sea-ice indices for 100-year scenarios. Illustration of sea-ice indices for years selected for the status quo (black) and the decreasing ice (grey) 100-year scenarios. The scenarios use the same set of data for the first 17 years (1996-2012) and then diverge

Once the 100-year sea-ice time series were selected, all needed forcing functions in Ecosim and Ecospace were constructed from existing data, using the same years of data as were selected for sea-ice. 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. 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).

Future Fishing Scenarios

Currently the only commercial fishery operating in the study area is the krill fishery. Under Conservation Measure (CM) 51-01, some form of which has been in place since 1991, the total allowable catch of krill for Statistical Subareas 48.1, 48.2, 48.4, and 48.4 combined is 5.61 million tonnes per season (CCAMLR 2010). Until the CCAMLR has agreed on a finer scale allocation between smaller management units, total krill catch in any one season is capped at the “trigger limit,” of 620,000 tonnes (CCAMLR 2010). With CM 51-07 the CCAMLR has further agreed to an interim distribution of the trigger limit such that no more than 25% of the trigger level, or 155,000 tonnes, can be caught in Statistical Subarea 48.1 (CCAMLR 2016). Since the 2012/2013 fishing season, fishers working in Statistical Subarea 48.1 have caught at least 90% of the trigger limit catch (CCAMLR 2017). It is likely that in future years, fishing nations will seek to expand catches beyond the trigger limit.

Four future fishing effort scenarios were developed. Each of the four fishing scenarios begins with the same 17 year effort time series, 1996-2012, that was reported to

the CCAMLR (CCAMLR 2017), the scenarios diverged for the remaining 83 years. The first scenario, which serves solely as a benchmark, represents the cessation of fishing after 2012, with zero effort entered for each time step after the end of year 17, and is referred to as fishing level “none”. The second scenario, meant to represent current level of fishing and is referred to as “status quo”, uses an 83-year loop of an “average year”. The average year represents the average monthly effort reported since CM 51-07 came into force (CCAMLR 2016) for the years 2009-2012. To create the remaining two scenarios, two multipliers were applied to the average year. The average total annual catch in Statistical Subarea 48.1 during this period was 115,249 tons. Ecopath with Ecosim, assumes that an increase in fishing effort will yield a proportional increase in catch (Christensen and Walters 2004). In the third scenario, referred to as 5x, the average effort year was multiplied by 5.37 to represent a scenario where 620,000 tonnes (the entire trigger limit) is caught in Statistical Subarea 48.1. In the fourth scenario, labelled as 12x, the average effort year was multiplied by 12.15 to represent 1.4 million tons. While the last fishing scenario represents dramatic, and currently unlikely, increases in fishing effort, the scale of increase is in line with the limitations set by CCAMLR. Specifically, it represents lifting the precautionary trigger limit (CCAMLR 2010) and allows exploration of fishers that catch 25% of the total allowable catch in Statistical Subarea 48.1 (CCAMLR 2016)

The krill fishery is dynamic and targeted areas change across months and years (Antarctic Ecosystem Research Division Southwest Fisheries Science Center and NOAA Fisheries 2016, CCAMLR 2017). Since the inception of the fishery, fishing activity has

shifted from occurring throughout most of Statistical Subarea 48. 1, to focusing on a few key locations (Nicol et al. 2012, Antarctic Ecosystem Research Division Southwest Fisheries Science Center and NOAA Fisheries 2016). While it is hard to predict where fishing activity might next concentrate, analysis of fishers' past activity indicate that they avoid fishing in icy waters (McElroy 1984), and specifically they rarely fish in areas with greater than 50% sea-ice concentration (Antarctic Ecosystem Research Division Southwest Fisheries Science Center and NOAA Fisheries 2016). Ecospace allocates fishing effort according to a gravity model that draws effort towards areas of high prey concentration and avoids high cost areas (Christensen and Walters 2004). Cost layers for the future scenario were created using the monthly sea-ice concentration maps (Cavalieri et al. 1996, updated yearly) and assigning high cost (value of 1,000) to cells with greater than 50% ice concentration. The first 17 years of the simulations used the observed SSMU fishing pattern as the cost layer (described above), while the remaining 83 years used ice concentration derived cost layers. Two cost layer time series were created, one to match the decreasing ice scenario and a second to match the status quo scenario.

Scenario Exploration

Eight scenarios (all combinations of sea-ice condition and fishing level) were run through Ecosim and Ecospace. Both Ecosim and Ecospace analyses were run to explore whether including spatial dynamics influenced biomass accumulation simulation outcomes. For each combination, the Ecospace scenario used the same time series for sea-ice index, open water, Chlorophyll *a*, and fishing effort as the Ecosim scenario of the same combination. Ecospace additionally included spatio-temporal dynamic maps of sea-

ice concentration, open water concentration, and fishing cost layers. All scenarios began with the same 17 years (1996-2012) of data and then diverged according to the combination of sea-ice conditions and fishing pressure.

Results

A spatial model was created that adequately recreated the spatial distribution of modeled species for the period 1996-2012. Additionally, 100-year simulations of all eight combinations of sea-ice condition and fishing level were run through Ecosim and Ecospace. All simulations were initiated with the same 17 years of data that had been used to calibrate the Ecosim simulation and tune the initial Ecospace run.

Spatial Model for 1996-2012

For the years 1996-2012, the spatial model's adequacy was assessed by visually comparing model output, to the tracking and sightings data that were used to create the distribution maps for each species. The goals were to ensure that over the course of the simulation, species did not disappear in the model from areas where they were observed in 2012 and, where data exist, to compare general spatial trends between the model and real life. When tuning and assessing the model, special focus was paid to the eight species that were used to calibrate the Ecosim simulations. After applying a linear response to sea-ice or open water, as appropriate for each species, the model was deemed adequate.

Antarctic fur seal pups have been counted and tagged annually at Cape Shirreff, on Livingston Island since 1992 (Goebel and Reiss 2014). Winter tracking data indicates

that fur seals use a large portion of Statistical Subarea 48.1 during the winter, but that they continue to concentrate near Cape Shirreff each summer during the breeding season (Goebel and Reiss 2014). Approximately 85% of fur seal pups born in Statistical Subarea 48.1 are born at Cape Shirreff (Hucke-Gaete et al. 2004, Goebel and Reiss 2014). Annual summer pup counts (Goebel and Reiss 2014) indicate that Antarctic fur seal biomass declined from 1996-2012. The distribution map used for Antarctic fur seals was intentionally biased to reflect the importance of the Cape Shirreff Colony; a 75 km radius around Cape Shirreff (Orange circle in Figure 27 A) was classed as the best habitat. The Ecospace simulation was considered adequate when the region around Cape Shirreff maintained its relative importance through the end of the tuning period (Figure 27 B) and when the simulation indicated an overall decline in fur seals (Figure 27 C).

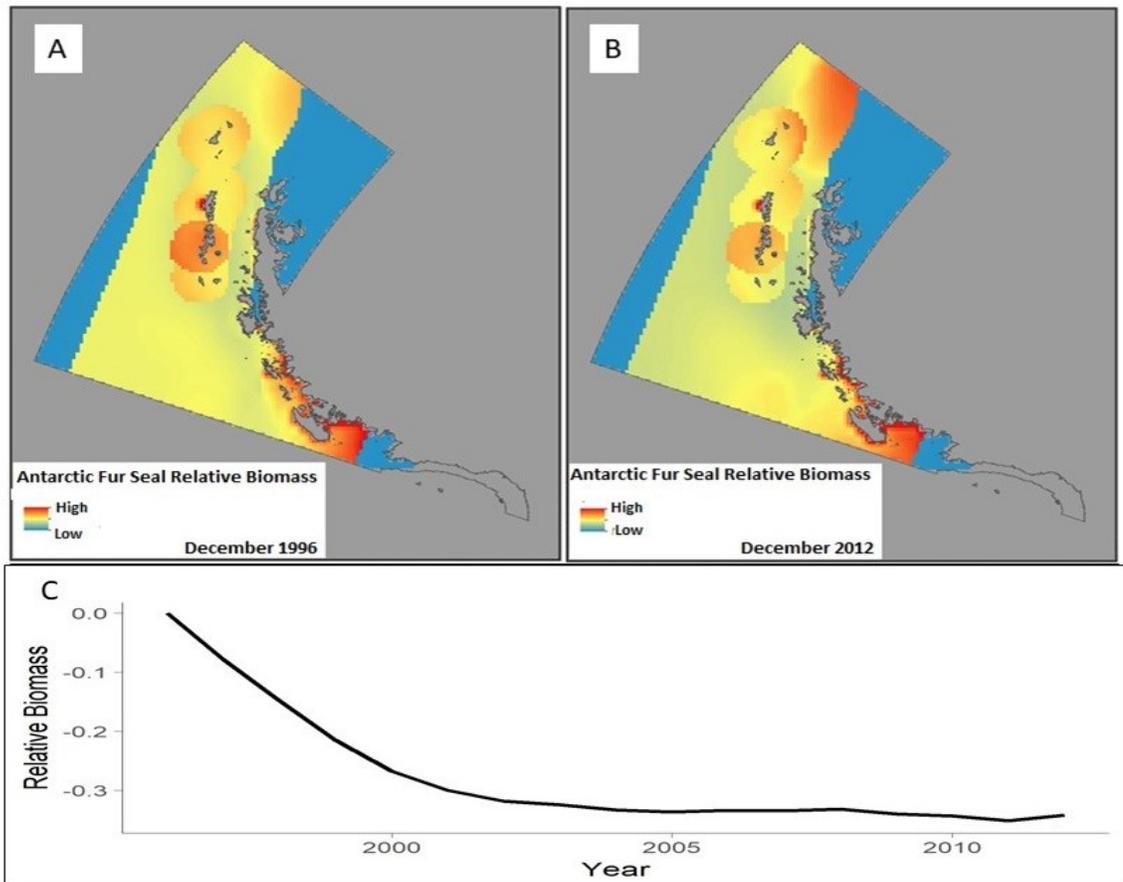


Figure 27. Ecospace simulation outcomes for fur seals 1996-2012. The maps illustrate spatial distribution simulation outcomes for Antarctic fur seals in December of 1996 (A) and December of 2012 (B). The graph in part (C) illustrates the change in log relative biomass over time. In graph C, the value 0.0 represents the starting relative biomass.

Adélie penguin colonies have been counted annually for more than 20 years by both NOAA-AMLR in the South Shetland Islands in the northern part of Statistical Area 48.1 (Trivelpiece et al. 2011, Hinke et al. 2014) and by the Palmer LTER near Anvers Island in the southern part of Statistical Area 48.1 (Ducklow et al. 2013). Chinstrap penguin colony nests have been counted annually for more than 20 years in the South Shetland Islands (Trivelpiece et al. 2011). Like Antarctic fur seals, Adélie and Chinstrap penguins are central place foragers, and aggregate around their colonies in the summer;

winter tracking data indicates that they use much larger areas when not required to return to their nests to feed chicks (Second WS-MPA Domain 1 2015). Region wide studies indicate that Adélie and Chinstrap penguin populations are in decline, with the more northern colonies experiencing the greatest impacts (Lynch et al. 2012). The Ecospace simulation was considered adequate when the foraging areas around all of the known colonies (coastal areas with higher relative abundance in Figure 28 A and Figure 29 A) persisted and maintained higher concentrations of biomass than surrounding areas through the end of the simulation, while the more southern colonies experienced increased relative biomass by the end of the simulation (Figure 28 B and Figure 29 B), and when the simulation indicated an overall decline in Adélie and Chinstrap penguins (Figure 28 C and Figure 29 C). Ecospace simulation outcomes for Chinstrap penguin include an area of higher concentration in the north-western Weddell Sea in December 2012 (Figure 29 B). Field data do not indicate that such a concentration exists in the real world (Hinke et al. 2015, Second WS-MPA Domain 1 2015). However, no sea-ice response curves were identified that resulted in the northern colonies remaining populated in December 2012 that did not also produce this area of concentration in the Weddell Sea.

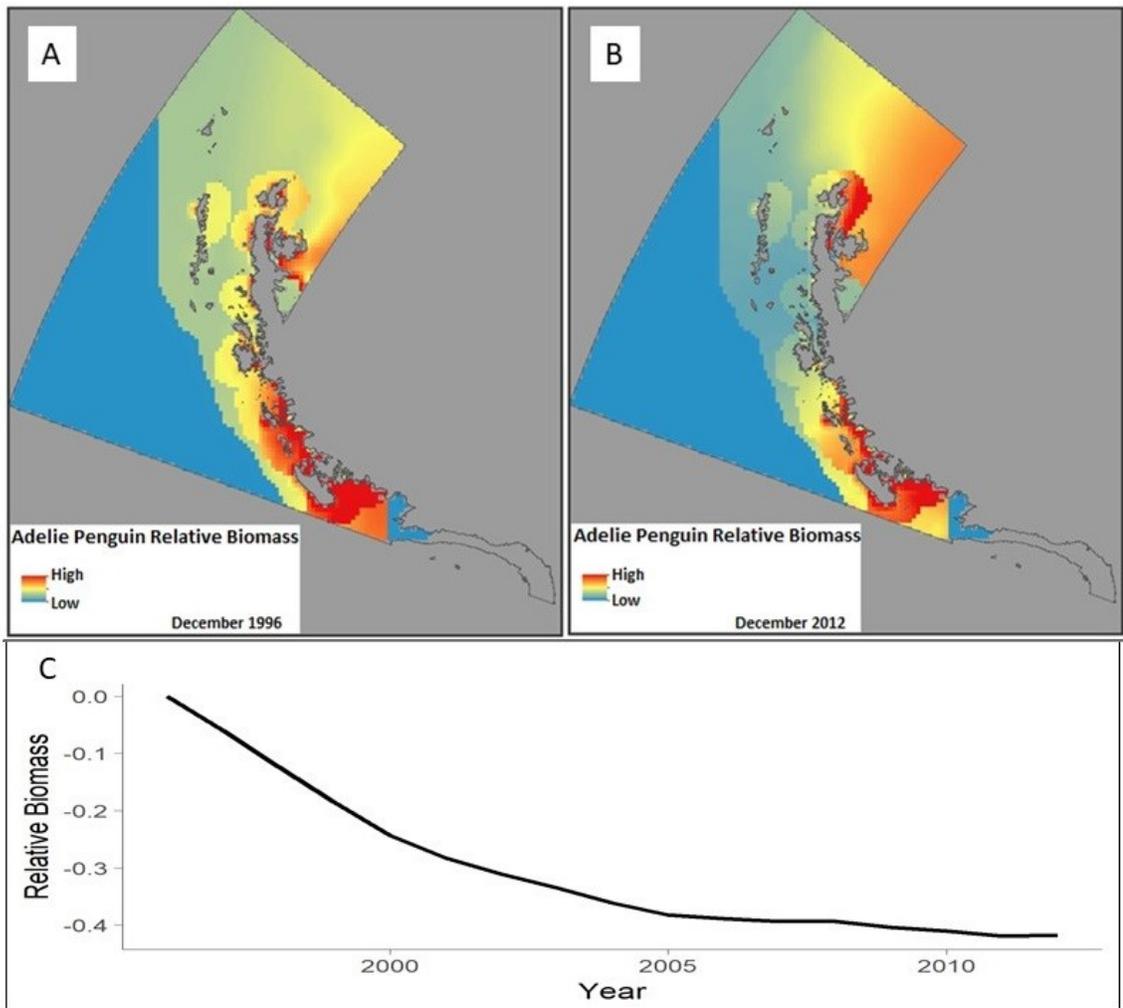


Figure 28. Ecospace simulation outcomes for Adélie Penguins 1996-2012. The maps illustrate spatial distribution simulation outcomes for Adélie penguins in December of 1996 (A) and December of 2012 (B). In these maps, redder cells indicate greater concentration of biomass. The graph in part (C) illustrates the change in log relative biomass over time. In graph C, the value 0.0 represents the starting relative biomass.

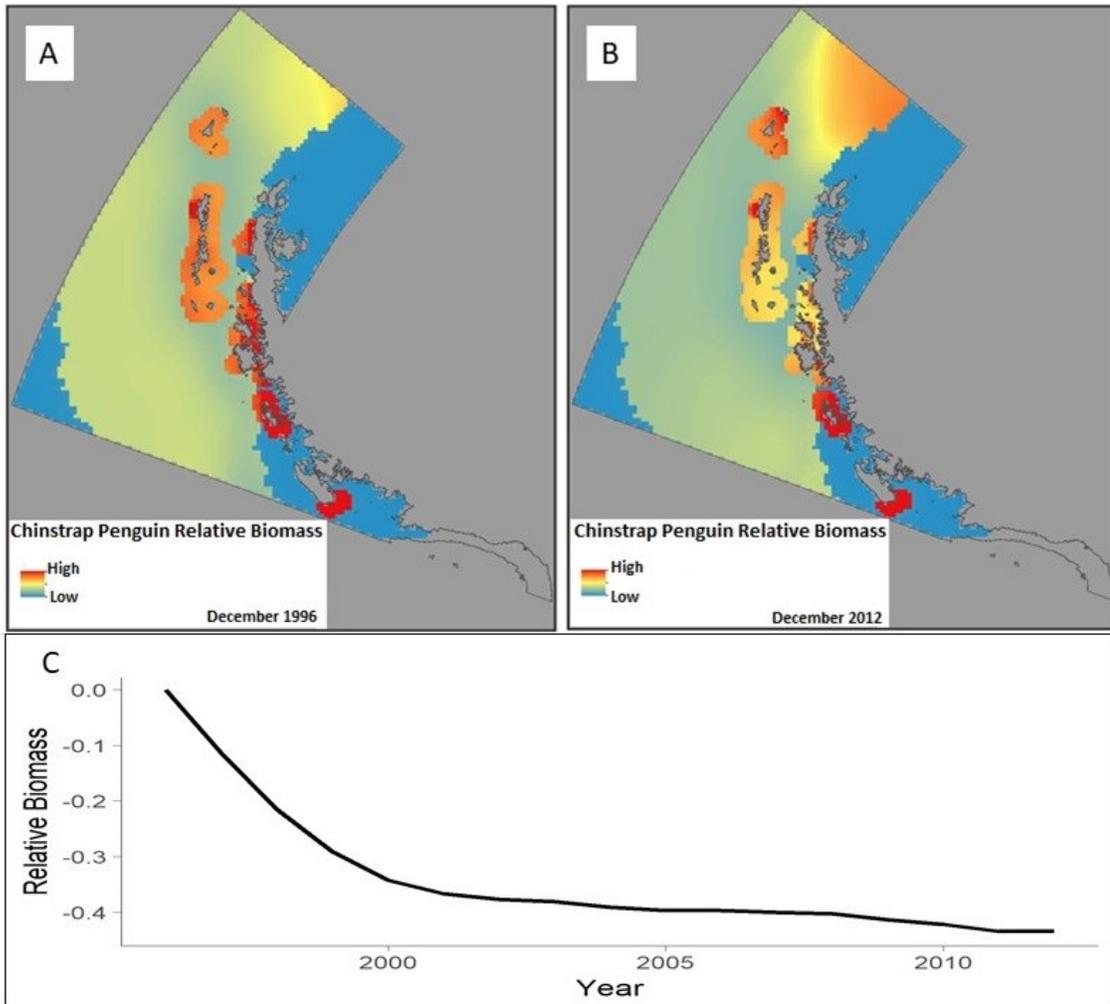


Figure 29. Ecospace simulation outcomes for Chinstrap Penguins 1996-2012. The maps illustrate spatial distribution simulation outcomes for Chinstrap penguins in December of 1996 (A) and December of 2012 (B). In these maps, redder cells indicate greater concentration of biomass. The graph in part (C) illustrates the change in log relative biomass over time. In graph C, the value 0.0 represents the starting relative biomass.

Gentoo penguin nests in the South Shetland Islands have been counted annually since 1984 by NOAA-AMLR (Pers. comm., J. Hinke, NOAA-AMLR., April 2015). Gentoo penguins are central place foragers and stay within a 25 km radius of their nests during the summer breeding season (Second WS-MPA Domain 1 2015). In the winter, their distribution expands, but tracking data indicate that Gentoo penguins do not roam as

widely or as far offshore as Chinstrap or Adélie penguins (Second WS-MPA Domain 1 2015). Region wide studies (Lynch et al. 2012) and local nest counts (Pers. Comm., J. Hinke, NOAA-AMLR., April 2015) indicate that the Gentoo penguin population is growing. The Ecospace simulation was considered adequate when the foraging areas around all of the known colonies (coastal areas with higher relative abundance in Figure 30 A) maintained a greater concentration of biomass than surrounding areas through the end of the simulation (Figure 30 B) and when the simulation indicated an overall increase in Gentoo penguin relative biomass (Figure 30 C).). Ecospace spatial outcomes for gentoo penguins include an area of higher concentration on the Eastern side of the Antarctic Peninsula in December 2012 (Figure 29 B). Field data do not indicate that such a concentration exists in the real world (Second WS-MPA Domain 1 2015). However, all open-water response curves tested that produced an increase in biomass also resulted in this area of concentration.

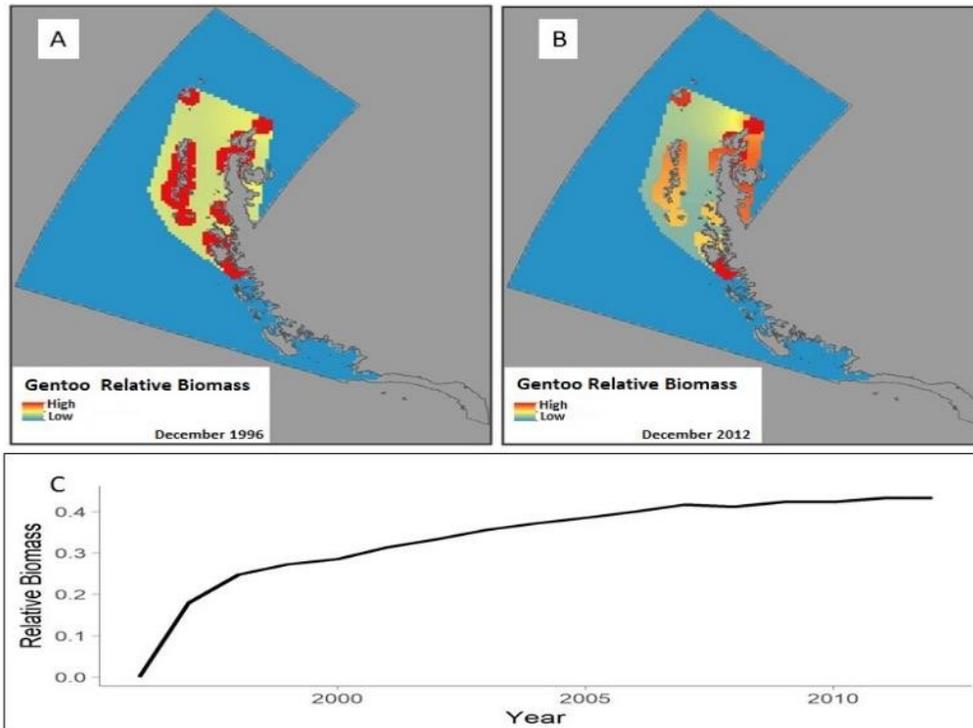


Figure 30. Ecospace simulation outcomes for Gentoo Penguins 1996-2012. The maps illustrate spatial simulation outcomes for Gentoo penguins in December of 1996 (A) and December of 2012 (B). In these maps, redder cells indicate greater concentration of biomass. The graph in part (C) illustrates the change in log relative biomass over time. In graph C, the value 0.0 represents the starting relative biomass.

C. gunnari and *N. rossii* abundances have been sampled irregularly since the late 1970s, with most sampling efforts concentrated around Elephant Island in the APEI SSMU (Kock and Jones 2005 and see Figure 8 above for location of the APEI SSMU). While sampling locations have been spatially constrained, potential *C. gunnari* and *N. rossii* habitat is thought to extend throughout much of the coastal regions of Statistical Subarea 48.1 (*N. rossii*: DeWitt et al. 1990, *C. gunnari*: Iwami and Kock 1990). Recent surveys indicate that abundance for both species has increased (Kock and Jones 2012). The Ecospace simulation was considered adequate when biomass for each species increased around Elephant Island over the course of the simulation (Figure 31 A and B

and Figure 32 A and B) and when the simulation indicated an overall increase in *C. gunnari* (Figure 31 C) and *N. rossii* (Figure 32 C) relative biomass. The model was not able to recreate a localized increase in biomass around Elephant Island; simulation outcomes indicate a much broader area of increase for both species

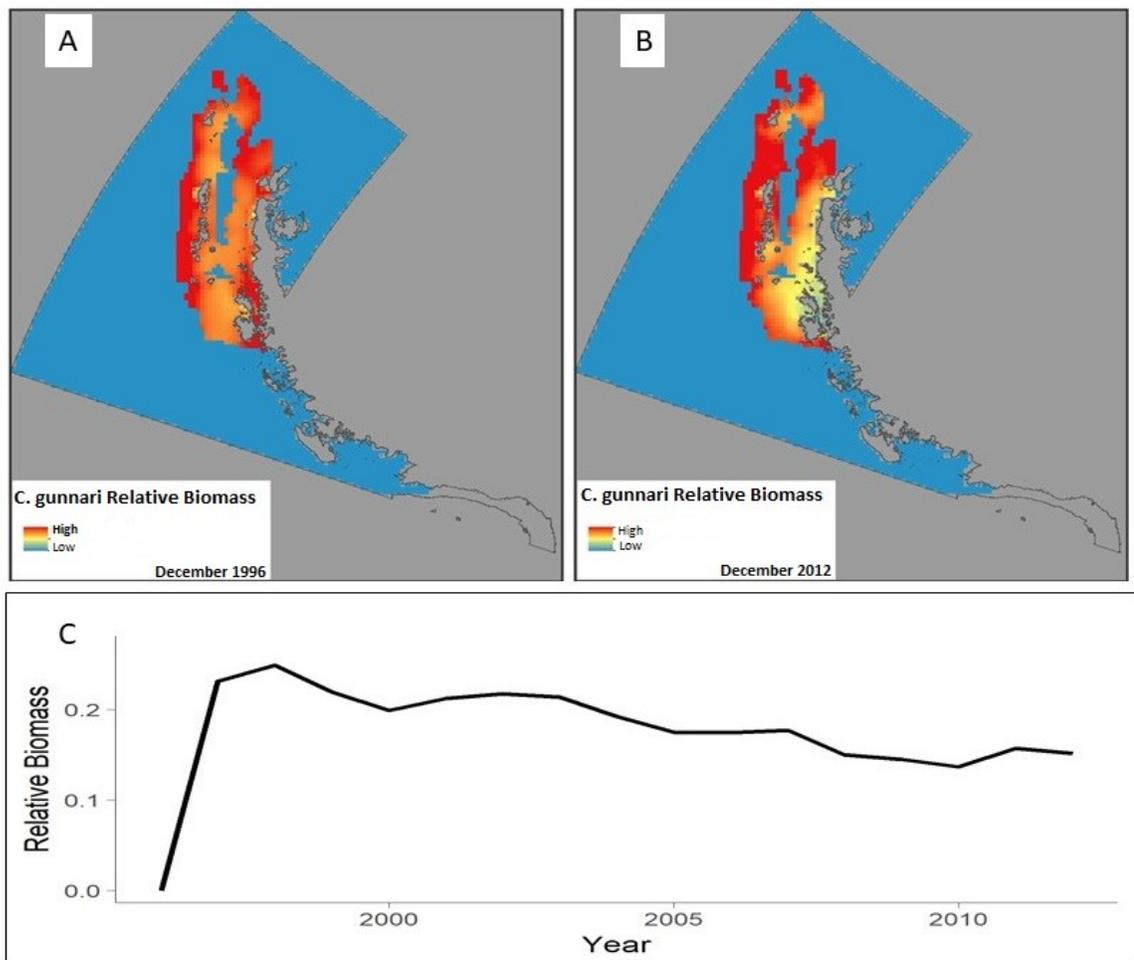


Figure 31. Ecospace simulation outcomes for *C. gunnari* 1996-2012. The maps illustrate spatial simulation outcomes for *C. gunnari* in December of 1996 (A) and December of 2012 (B). In these maps, redder cells indicate greater concentration of biomass. The graph in part (C) illustrates the change in log relative biomass over time. In graph C, the value 0.0 represents the starting relative biomass.

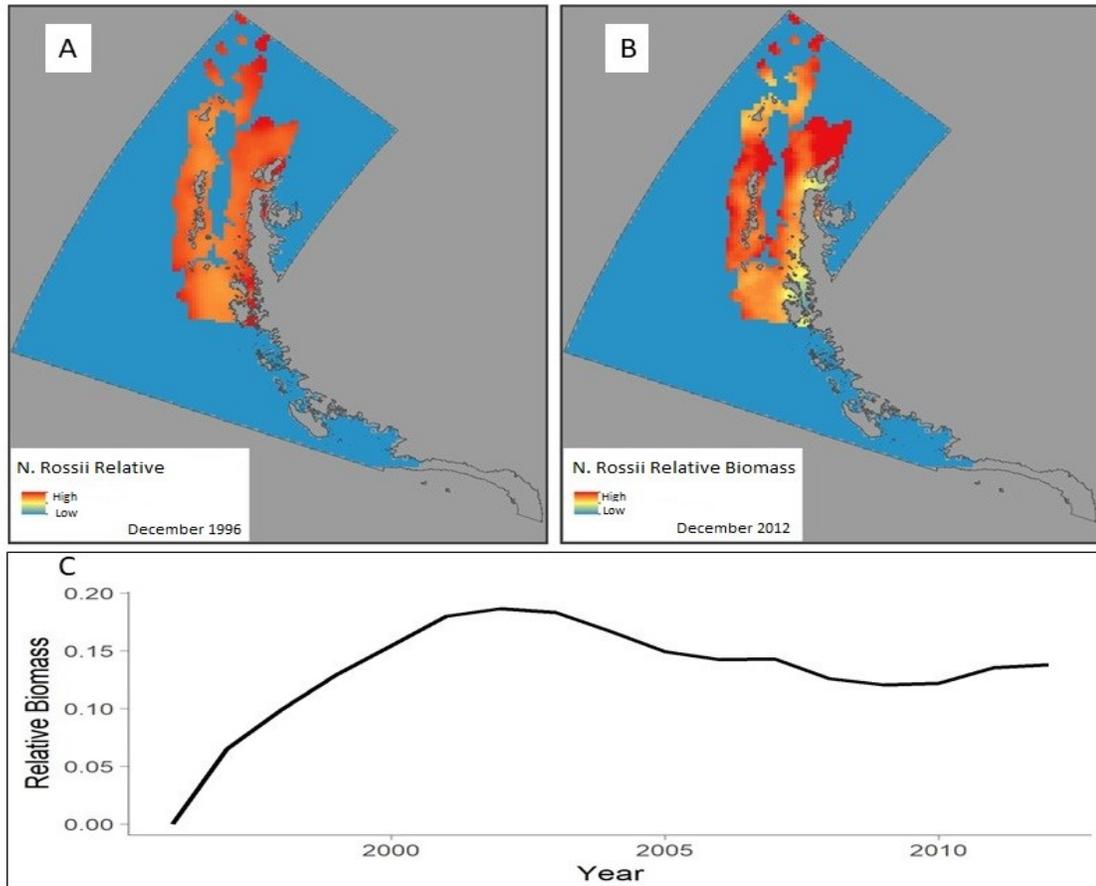


Figure 32. Ecospace simulation outcomes for *N. rossii* 1996-2012. The maps illustrate spatial simulation outcomes for *N. rossii* in December of 1996 (A) and December of 2012 (B). In these maps, redder cells indicate greater concentration of biomass. The graph in part (C) illustrates the change in log relative biomass over time. In graph C, the value 0.0 represents the starting relative biomass.

Similar to both *C. gunnari* and *N. rossii*, surveys to sample *G. gibberifrons* have been conducted irregularly and have been restricted in space to the area near Elephant Island (Kock and Jones 2005). It is likely that habitat exists for the species throughout much of the coastal regions of Statistical Area 48.1 (DeWitt et al. 1990). Recent surveys conducted near Elephant Island indicate that the biomass of *G. gibberifrons* has

decreased (Kock and Jones 2012). The Ecospace simulation was considered successful when the area around Elephant Island showed a decrease in relative importance (Figure 33 A and B) and the simulation indicated and overall decline in relative biomass (Figure 33 C).

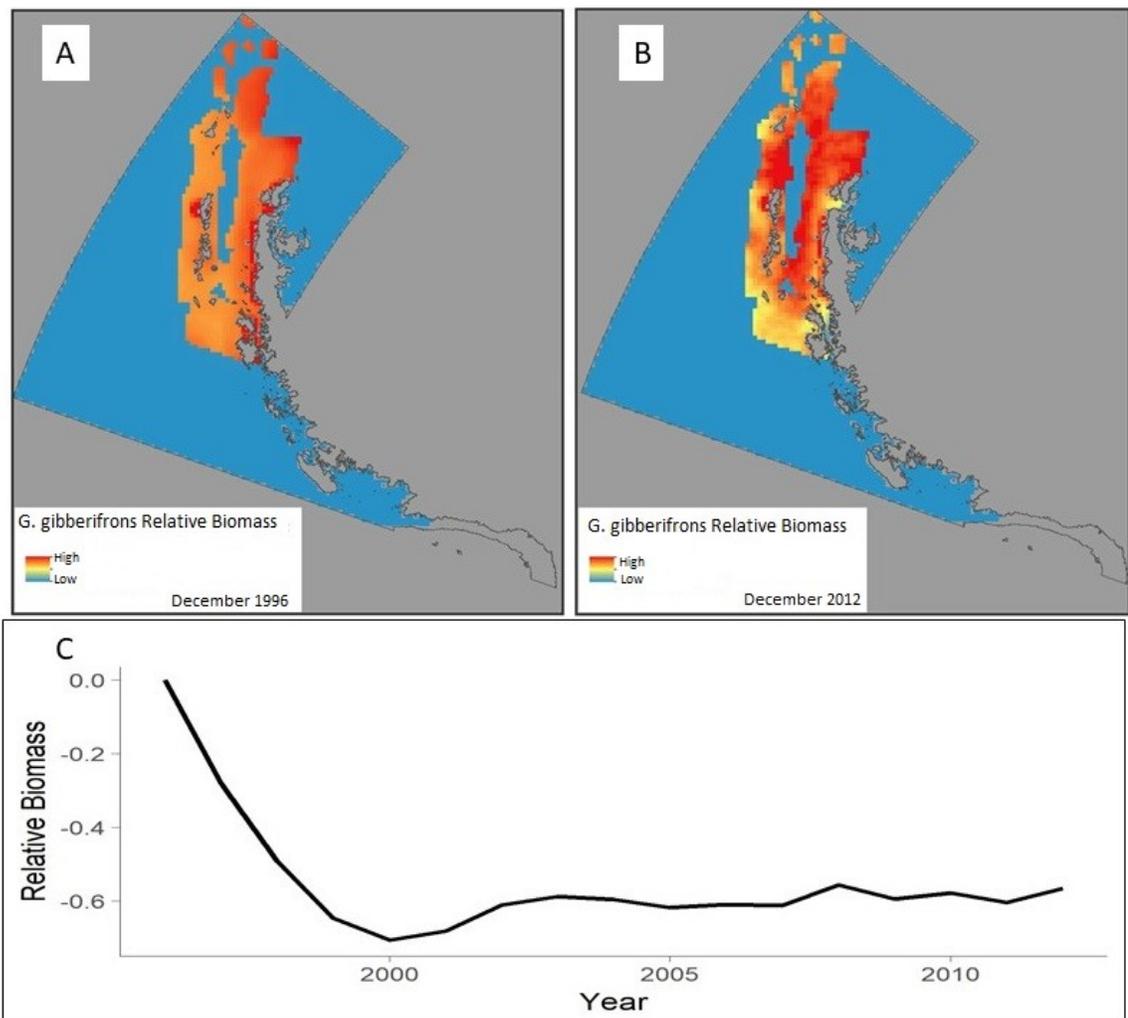


Figure 33. Ecospace simulation outcomes for *G. gibberifrons* 1996-2012. The maps illustrate spatial simulation outcomes for *G. gibberifrons* in December of 1996 (A) and December of 2012 (B). In these maps, redder cells indicate greater concentration of biomass. The graph in part (C) illustrates the change in log relative biomass over time. In graph C, the value 0.0 represents the starting relative biomass.

Large krill in Statistical Subarea 48.1 have been sampled by several research groups using nets and fisheries acoustics. Work was conducted during the Antarctic summers and began in the early 1990s. Data were standardized and combined for all sample years to create a density raster (Second WS-MPA Domain 1 2015). From 2012-2016, NOAA-AMLR conducted winter acoustic and net surveys in the northern part of Statistical area 48.1 (Reiss et al. 2017). Across all seasons, krill abundance in the region is thought to be declining with larger concentrations of krill appearing in more southern parts of the region (Atkinson et al. 2004, Reiss et al. 2008, Atkinson et al. 2009, Reiss et al. 2017). The winter surveys further illustrated that swarms of krill contract into the more coastal regions in the winter (Reiss et al. 2017). Though every attempt was made, the model was unable to capture this seasonal pattern (Figure 34 A, B and C). Ecospace currently does not allow for directional movement of modeled species (Christensen and Walters 2004). Though the software allows users to slow species' relative dispersal into bad habitat, the dispersal speed has relative little impact on spatial distribution patterns (Christensen and Walters 2004). While an advection module exists in the software, it is not fully operational, and tests with it using the best available windspeed data resulted in krill being flushed from the system in less than two years. As a result, directional movement of krill was not included in the Ecospace simulations, and the simulations were unable to recreate the winter contraction to near shore waters. The model adequately recreated the increasing relative importance of more southern areas (Figure 34 A and C) and the overall decline in krill biomass (Figure 34 D).

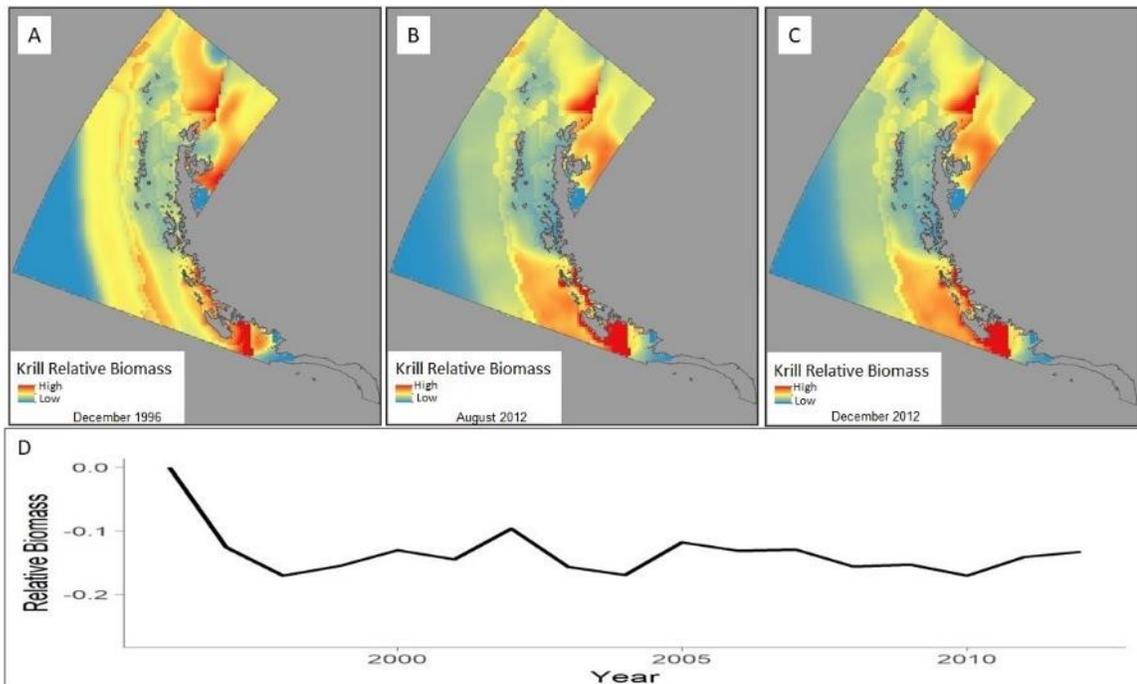


Figure 34. Ecospace simulation outcomes for Large Krill 1996-2012. In these maps, redder cells indicate greater concentration of biomass (within the map). Note that the map for August 2012 (Winter) has a similar concentration of krill biomass in coastal areas as illustrated in the map for December 2012 (Summer). The graph in part D illustrates the change in log relative biomass over time. In graph D, the value 0.0 simply represents the starting relative biomass.

Future Scenarios

Eight 100-year duration time dynamic simulations were run in Ecosim and Ecospace to investigate the impact of decreasing sea-ice conditions and increasing fishing effort on temporal biomass accumulation patterns. The eight scenarios represented all combinations of sea-ice scenario (status quo and decreasing ice) and four levels of fishing pressure (none, status quo, 5x and 12x) The 100-year scenarios were run both in Ecosim and Ecospace. Monthly cost layers were fed into the model using the external data framework and differed across the two ice scenarios. All simulation runs began with the

same 17 years of data (1996-2012) and then diverged according to the specific combination of sea-ice conditions and fishing pressure.

Ecosim results for the eight species which were used to calibrate the Ecosim simulations (Chapter 2) are presented below (Figure 35). With the exception of *G. gibberifrons*, both the sea-ice regime and the level of fishing effort impacted the relative biomass simulation outcomes for each species. *G. gibberifrons* experienced a steep decline and did not recover, regardless of conditions. Sea-ice conditions appeared to be more important in determining population trajectory as simulation outcomes clustered by sea-ice scenario; fishing effort level worked to stratify the simulation outcomes within each ice scenario. Fishing level did not change the trajectory of biomass accumulation patterns, it merely altered the magnitude of increase or decline. This pattern where sea-ice scenario determines the trajectory and fishing pressure scales the response, resulted from just one randomly selected status quo sea-ice scenario and one randomly selected decreasing ice scenario. It is possible that re-running the simulations with a different set of randomly selected years populating the sea-ice scenarios would yield a different result.

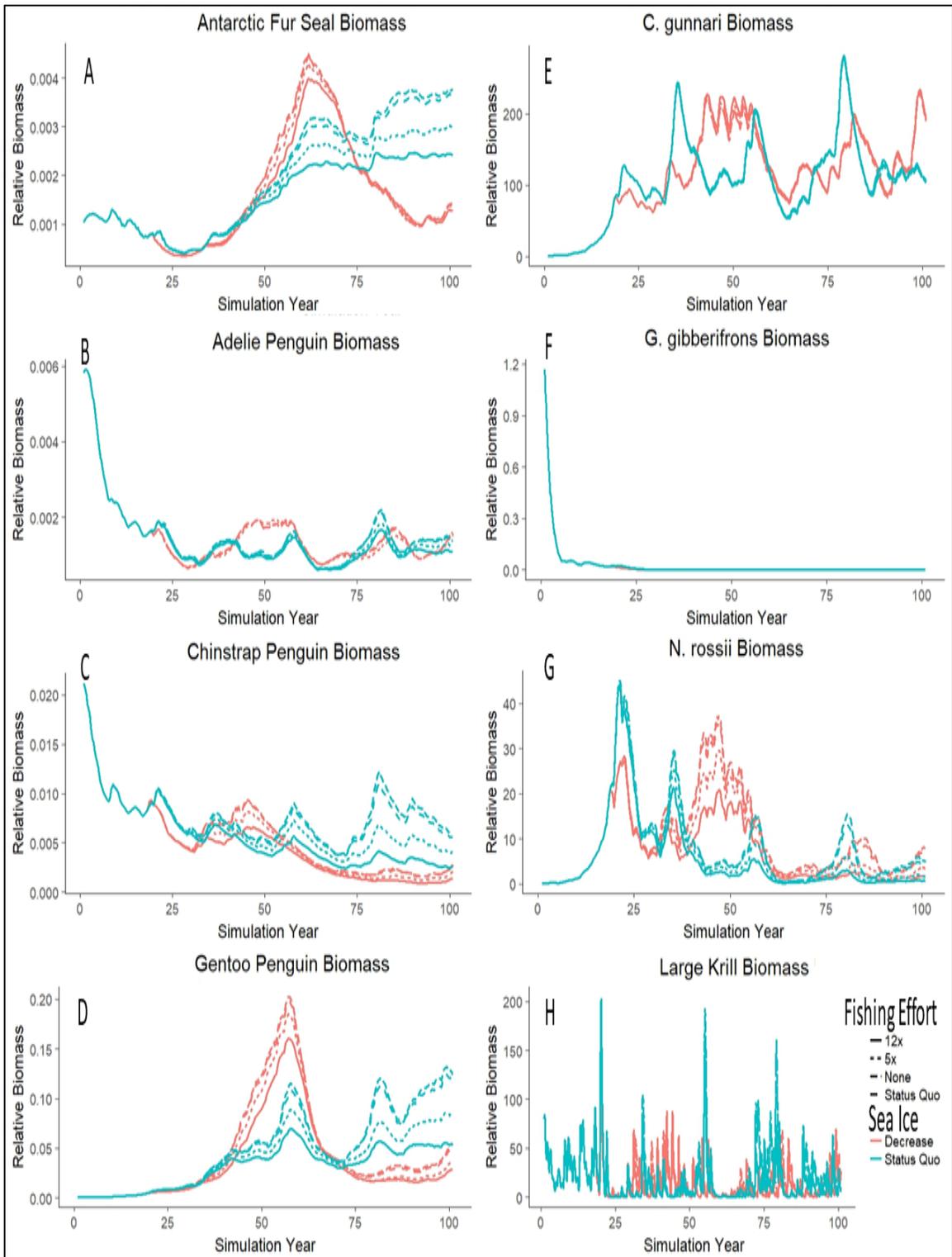


Figure 35. Results of 100-year Ecosim simulations. Shown are the results for the eight species used to calibrate the model. In all panels, the color represents the sea-ice scenario and the line type represents the fishing level.

Following years of decline, Ecosim simulation outcomes for Antarctic fur seals indicate a significant rise in relative biomass starting approximately 25 years into the scenario, regardless of sea-ice scenario or fishing effort. Then at approximately year 65 in the simulation, Ecosim simulation outcomes indicate either a leveling off (status quo ice conditions) or a decline (decreasing ice conditions) of fur seal relative biomass. The simulations further indicate a steep increase in Antarctic fur seal relative biomass at the same time the simulation outcomes indicate a steep decrease in leopard seal relative biomass and several years of modestly higher relative krill biomass. In contrast, the simulation outcome for levelling off or renewed decline occurs at the same time that the model indicates several years of lower large krill relative biomass (Figure 36). These simulation outcomes are consistent with the hypothesis that the fur seal colony at Cape Sherriff is controlled by both top down (predatory) and bottom up (prey availability) forces (Goebel and Reiss 2014).

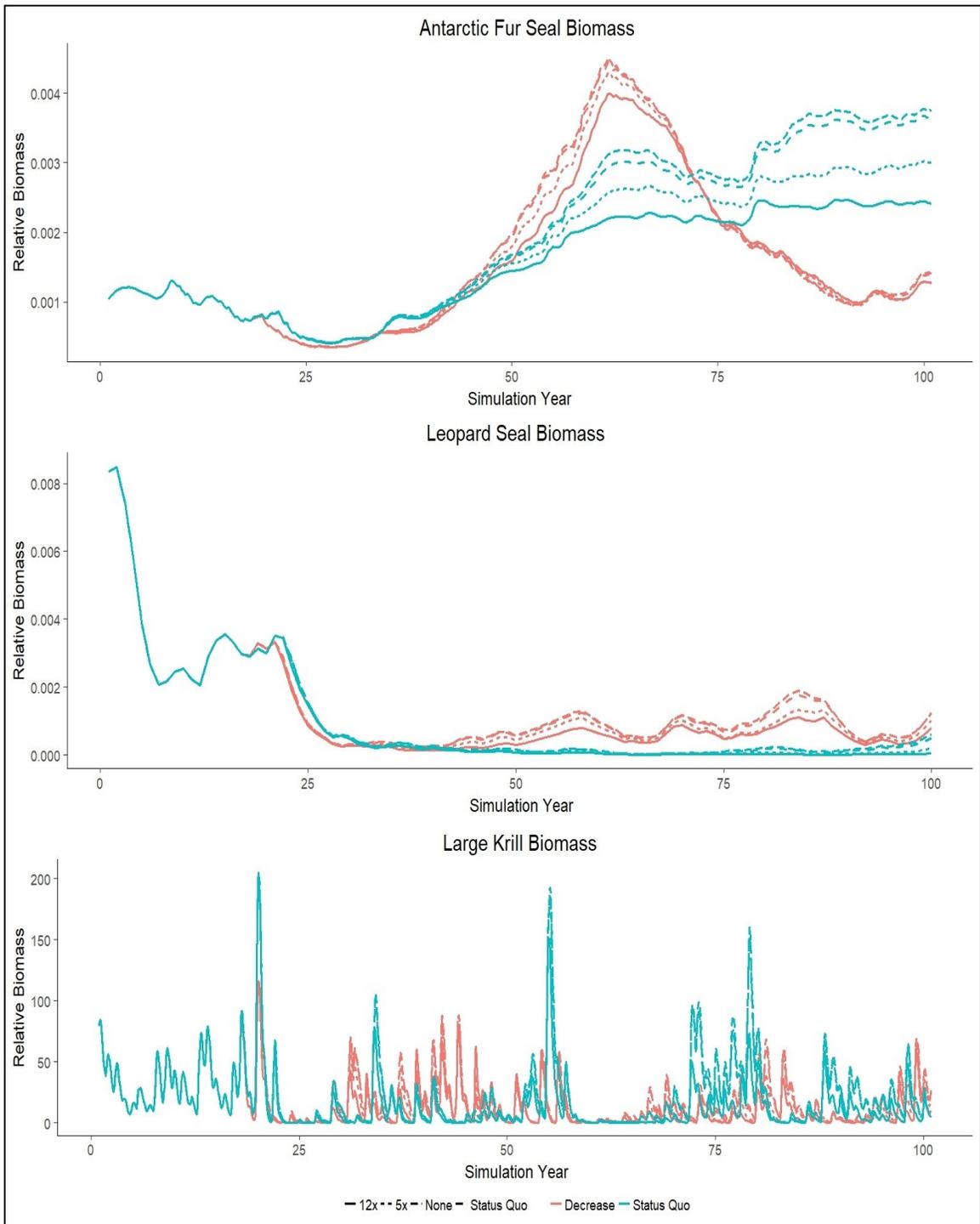


Figure 36. Comparison of predator and prey biomass 100-years Ecosim simulation outcomes. Stacked time dynamic simulation outcomes for Antarctic fur seals (A), Leopard Seals (B) and large krill (C) illustrate the correlation between changes in fur seal relative biomass, their predator (leopard seals) and key prey item (krill). The colors illustrate the different sea-ice scenarios; line type illustrates fishing level.

Running the same scenarios in Ecospace yielded simulation outcomes clustered by fishing level and stratified by ice status (Figure 37); this is the opposite pattern that was evidenced in Ecosim outcomes. The Ecospace results imply that the impact of fishing is greater when the spatial aspects of fishing are considered. Sea-ice scenario still has an impact, it is simply not as strong as it was when the spatial aspects of sea-ice and fishery were not considered. The difference between the Ecosim and Ecospace biomass outcomes might be explained by the fact that in Ecospace, modeled species are able to respond to sea-ice concentration patterns and move with into areas of higher quality habitat. Such movement patterns could soften the impact of environmental drivers and increase the importance of fishing levels on biomass and spatial simulation outcomes. Additionally, the Ecospace simulations were only visually tuned. It is possible that sea-ice and open water response curves were not drawn as accurately in Ecospace as they were in Ecosim, and this may have masked some of the true effects of these drivers.

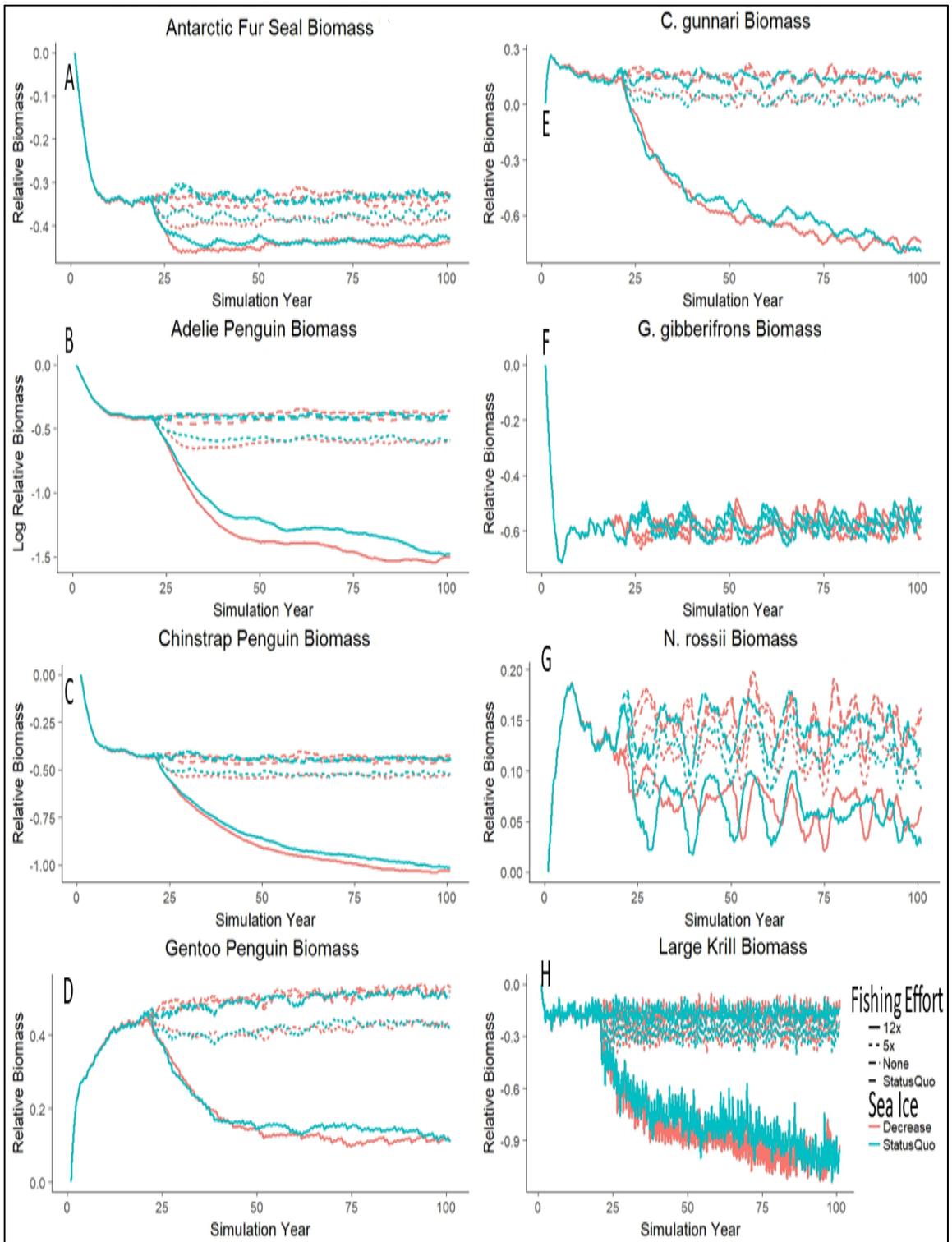


Figure 37. Results of 100-year Ecospace simulations. Results for the eight species used to calibrate the model. The value 0.0 represents the starting biomass, and values on the y axis represent a deviation from the starting biomass.

The spatial distribution of the eight monitored species changed little across simulations, with the largest difference noted across fishing levels. This is consistent with the pattern observed in the Ecospace simulation outcomes for relative log biomass. The use of species-specific distribution maps, constrains where species could appear and may have contributed to the large similarities in spatial distribution patterns across and between scenarios. In general, for krill (Figure 38. and Figure 39.) and other ice dependent species (Appendix 6) the areas of greatest biomass concentration shifted south and towards the Western edge of the icy Weddell Sea. These are areas that are often ice covered even in the summer. However, during the low ice years, these areas experience low ice concentrations (Cavalieri et al. 1996, updated yearly, Stammerjohn 2013) and would be accessible to the fishery. Ice dependent species like krill concentrate in these icy areas in the real world (Atkinson et al. 2004, Atkinson et al. 2009) and the model captures that behavior. Under the highest fishing effort level, the southern areas lose their relative importance to krill. Figure 40. Comparison of the input cost layer and output Ecospace effort in December of year 20 and Year 40. illustrates the cost layer input and Ecospace outcomes for effort at two time steps, December year 20 and December year 40, under decreasing ice conditions at the 12x fishing level. At year 20, the southern concentration of krill is still present and the southern areas experience low sea-ice concentration which is translated as low cost to the fishery. In such conditions, Ecospace simulations indicate that fishing effort would concentrate in this region (Figure 40. Comparison of the input cost layer and output Ecospace effort in December of year 20

and Year 40.). By year 40, the southern concentration of krill has dispersed (Figure 39). Even though sea-ice concentration is low in the southern region during year 40, the gravity model directs fishing effort to the more northern concentration of krill in the Weddell Sea. For the remainder of the simulation under 12x fishing pressure, the area of greatest krill concentration and fishing effort concentration remains in this more northern area. Ecospace simulation outcomes do not indicate that the southern krill concentration will reform.

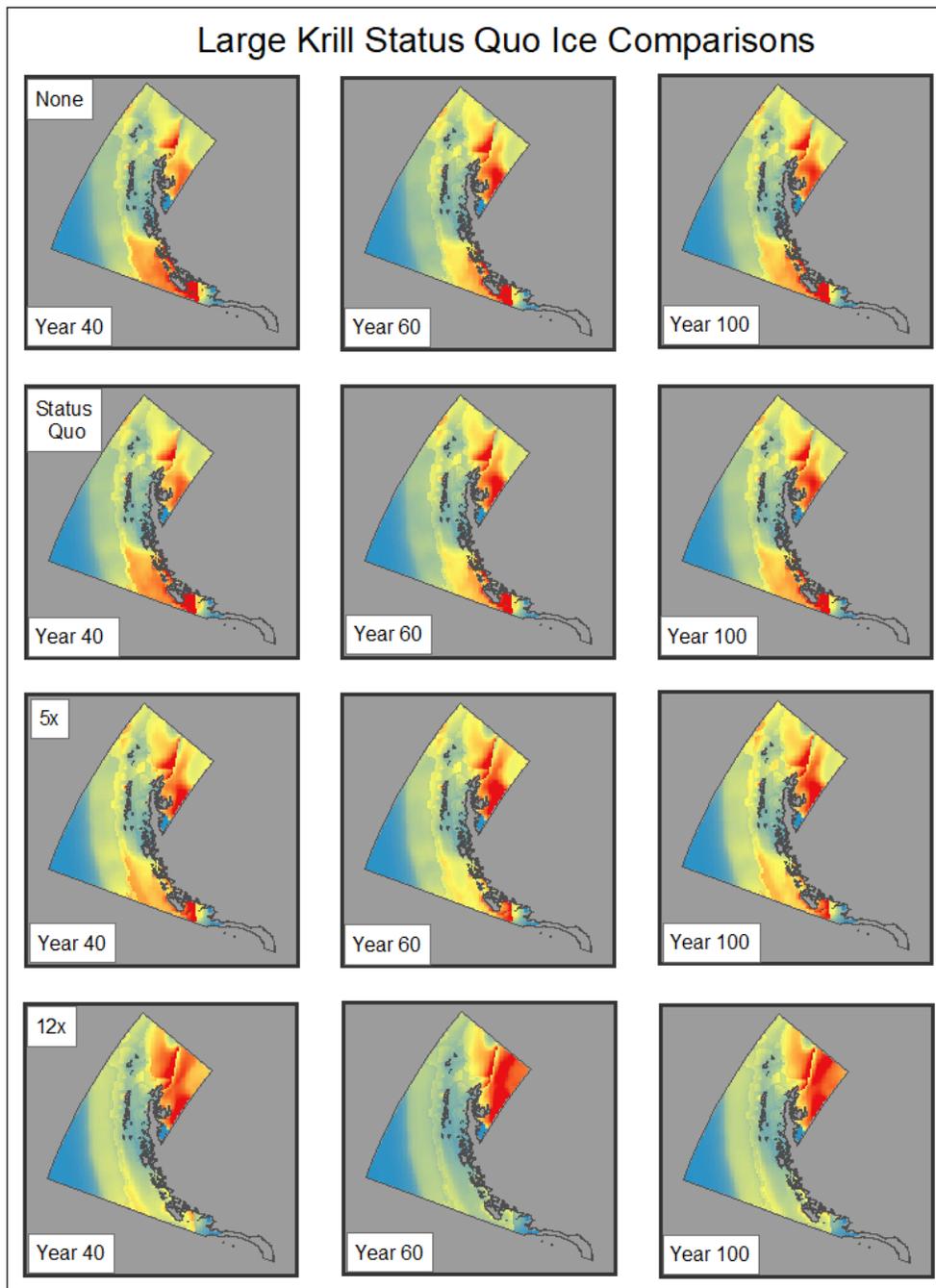


Figure 38. Spatial simulation outcomes for Large Krill in status quo ice conditions. Red color in maps indicated areas of higher relative importance.

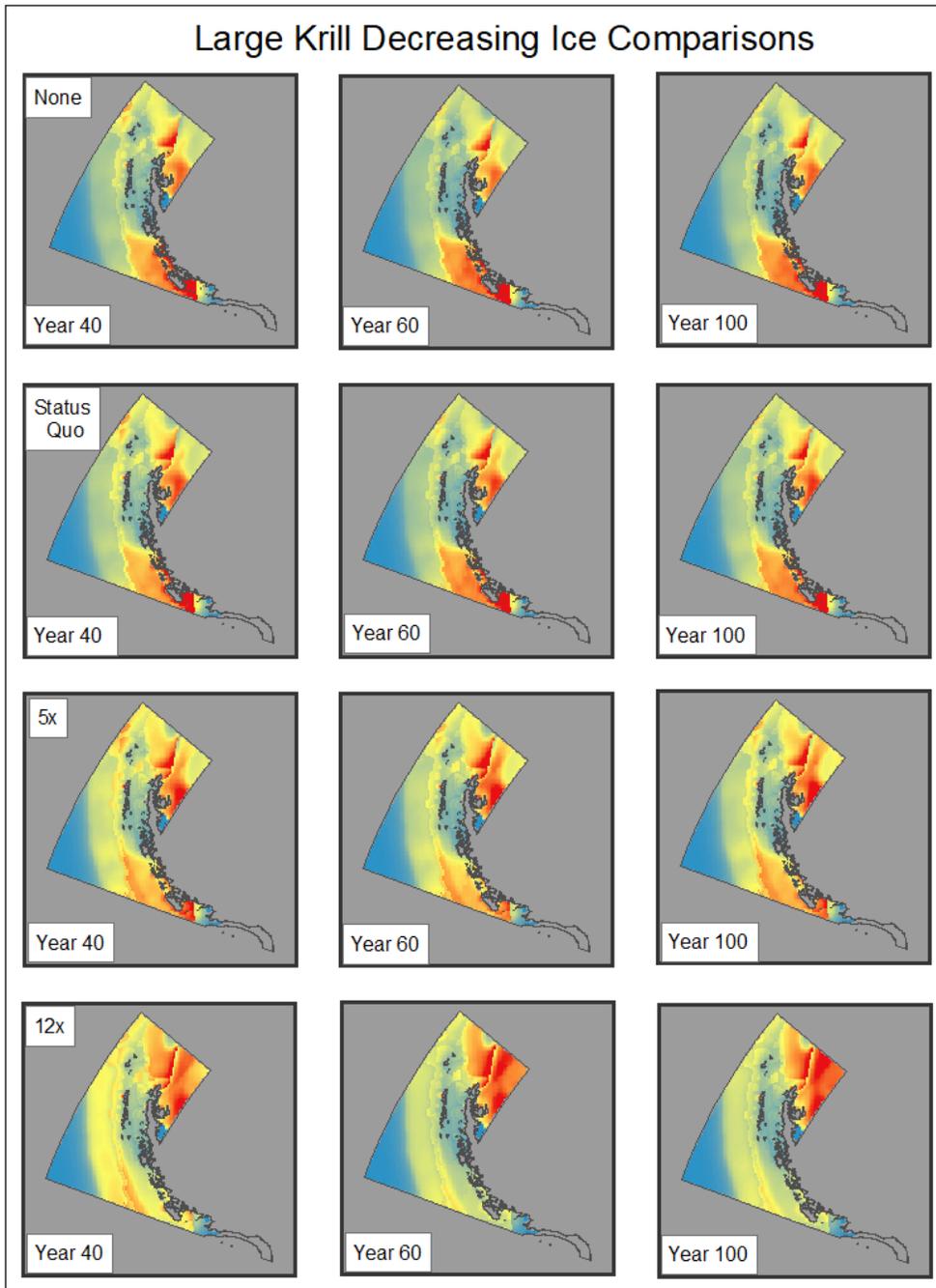


Figure 39. Spatial simulation outcomes for Large Krill in decreasing ice conditions. Red color in maps indicated areas of higher relative importance.

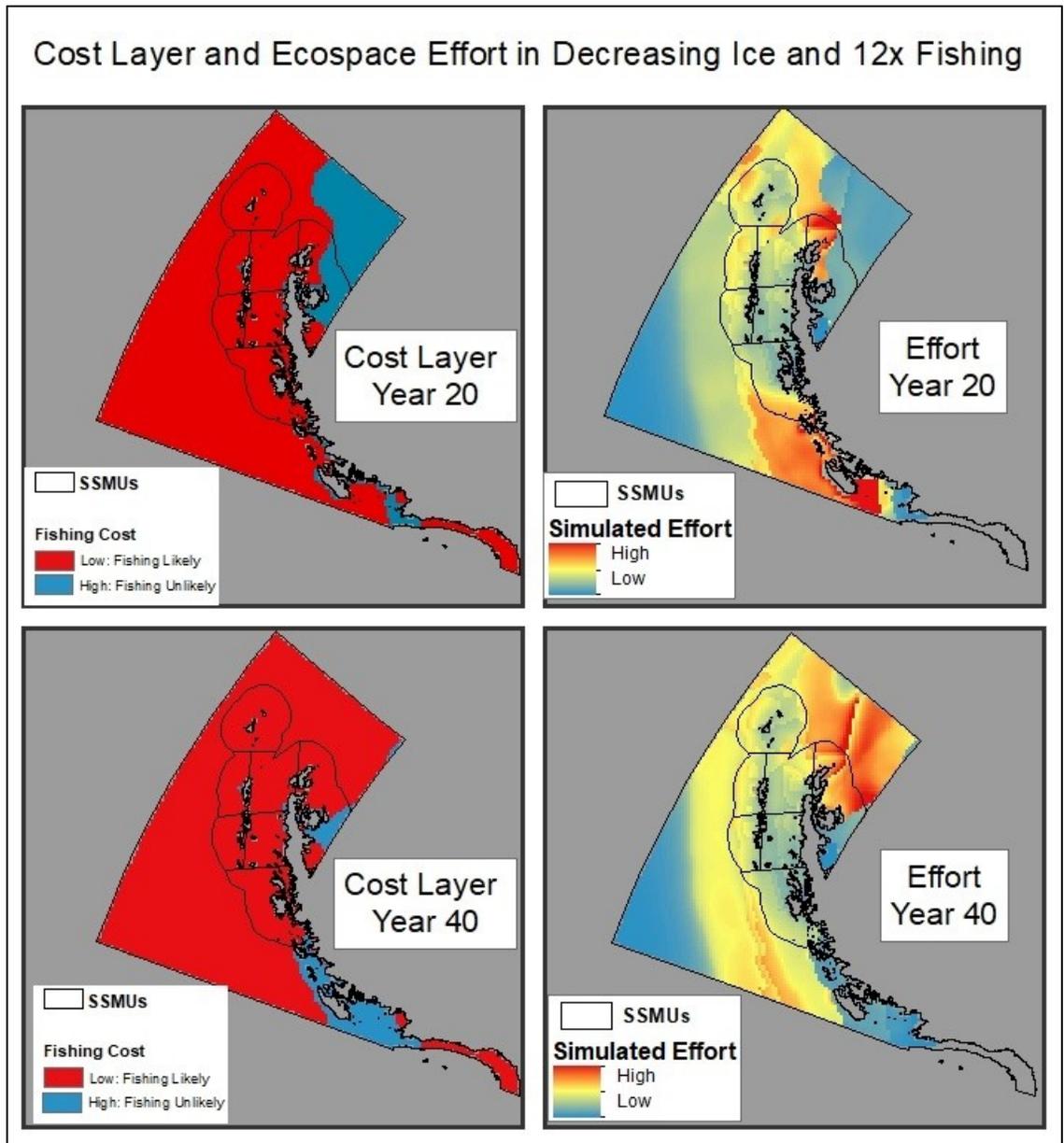


Figure 40. Comparison of the input cost layer and output Ecospace effort in December of year 20 and Year 40.

Discussion

The study successfully created a spatio-temporal model that adequately reflects conditions for the eight monitored species during the years 1996-2012. This model is therefore suitable to use to explore potential impacts of changing sea-ice and fishing

conditions. When comparing simulation outcomes for relative biomass across scenarios some general patterns emerge. Specifically, some species appear unlikely to recover to 1996 levels, even if all fishing ceases. Both fishing effort level and sea-ice conditions influence simulation outcomes for biomass. When only temporal dynamics are considered, sea-ice scenario has a more prominent signal than fishing pressures. However, when spatial patterns are considered, fishing effort level appears to have higher importance than sea-ice concentration. The implication of this result is that both intensity and spatial pattern of fishing are important in influencing biomass patterns for the targeted species (krill) and other members of the ecosystem. To help carry out the Ecosystem Based Management (EBM) approach defined in Article II of the CAMLR Convention (Convention on the Conservation of Antarctic Marine Living Resources 1980), the CCAMLR may find it productive to consider both the intensity and spatial distribution of fishing effort when making fisheries management decisions.

The Ecospace simulations were deemed to adequately recreate observed trends in biomass patterns for the eight monitored species for the years 1996-2012. However, it is worth noting a few limitations. Foraging area maps, which represent areas where animals are known or suspected to forage, were entered into the habitat capacity module, and influenced where Ecospace would allocate biomass. The input foraging maps were drawn to be inclusive of all areas that the animals are suspected to use, to allow for changes in spatial distribution patterns in response to environmental drivers. However, cells that were assigned a near zero value in the input would be far less likely to experience biomass concentrations, even as sea-ice conditions change. Further, the model produced some

unexpected results that do not align well with field observations and maybe related to the simulation of krill. The model's inability to re-create directional movement pattern of krill may be particularly problematic as some krill predators may be sensitive to changes in krill availability patterns (Reid et al. 2005, Watters et al. 2013). Simulation outcomes seem to reflect this sensitivity. Ecospace simulation outcomes indicate concentrations of chinstrap and Gentoo penguins east of the Antarctic Peninsula, where they are not known to concentrate in the real world (Hinke et al. 2015, Second WS-MPA Domain 1 2015) but where the model also indicates that krill reliably concentrate. It is well established that uncertainty related to krill movement patterns should be considered when developing spatial ecosystem models for the region, (Hill et al. 2007, Watters et al. 2013), yet the current Ecospace modelling framework does not allow for directional movement of krill. It is therefore challenging to account for, or directly consider, uncertainty related to krill movement patterns. It is possible that errors associated with simulation outcomes for krill impact krill predators indirectly through the modeled trophic interactions.

Ecospace simulation outcomes for the three modelled fish species, *C. gunnari*, *N. rossii*, and *G. gibberifrons* should also be viewed critically. Most of the scientific fishing effort and data describing these species, were centered on Elephant Island (Kock and Jones 2005), yet their habitat extends through a much broader portion of the Antarctic shelf region (DeWitt et al. 1990, Iwami and Kock 1990). The Monte Carlo trials in Chapter 2 indicated that the greatest sensitivity in model was attributed to the fish species, and this likely carries over for Ecospace simulation outcomes.

The 100-years simulations illustrate that Adélie penguins, Chinstrap penguins, and *G. gibberifrons*, all experience significant declines regardless of sea-ice conditions or fishing effort level. Even in the absence of fishing these species are unable to recover to 1996 levels. This pattern holds true for both the Ecosim time dynamic simulations and the spatially explicit Ecospace simulations. Watters et al. (2013), working in a different ecosystem modeling framework (the Foosa 0.0 package in R), produced a similar result; penguins did not recover to initial input biomass levels. The Foosa modeling framework allowed for the inclusion of depensation. Watters et al. (2013) explored different recruitment scenarios and concluded that depensatory processes were preventing penguin recovery. Neither the simulations run in Ecosim or Ecospace directly considered depensatory processes, but rather focused on trophic interactions. Yet both modeling frameworks produced the the same result, that penguins are unlikely to recover even in the absence of fishing. This implies that there may be several forces preventing penguin recovery.

The finding that some species are unlikely to recover has significant implications for MPA planning and evaluation. MPA planning would more productively focus on how implementation of an MPA could assist in maintaining sustainable fisheries in the face of climate change. If using Ecospace as the decision support tool, this may translate to conservation goals being set in terms of slowing indicated declines.

Large krill exhibit an overall decline across all scenarios. However, in the decreasing ice scenario, krill experience a slightly less severe biomass decline than in the status quo ice scenario. Considering that krill are known to be ice dependent (Everson

2000, Atkinson et al. 2004, Atkinson et al. 2009) it is perhaps counterintuitive that the lower ice scenario outcomes indicate a greater ending biomass of krill than the status quo ice scenario. It is possible that krill predator biomass declines so much under decreased ice conditions, that relief from predation pressure allows krill biomass to be slightly larger in decreased ice conditions. This is one possible hypothesis that is consistent with the modeling structure put forward here, but other hypotheses derived from different modeling frameworks could explain this pattern as well. For example Melbourne-Thomas et al. (2016) found that in declining sea-ice conditions, suitable habitat for larval krill may increase which could lead to larger than otherwise anticipated krill biomass estimates.

Field observations indicate that Antarctic fur seals at Cape Shirreff have been declining since about 2004 and that this decline is likely attributable to increasing Leopard seal predation and decreased availability of krill (Goebel and Reiss 2014). Ecosim tracks this decline for the years that data are available, and then in the 100-year scenarios, simulation outcomes indicate that fur seal relative biomass will suddenly increase approximately 25 years into the simulation. This increase in relative biomass is indicated in simulation outcomes regardless of sea-ice scenario or fishing effort. The simulations also subsequently indicate either a levelling off (status quo ice conditions) or a decline (decreasing ice conditions) at approximately 65 years into the simulation. Taken in isolation, this simulation outcome is unexpected. However, the Ecosim simulation outcomes indicated an increase in fur seal biomass after a steep decline in one of their predators, leopard seals, and following several years of modestly higher krill biomass.

The simulation outcomes indicated a levelling off or renewed decline of fur seals relative biomass at the same time as several years of particularly low krill relative biomass.

Ecosim simulation outcomes are therefore consistent with Goebel and Reiss (2014) that the fur seal population in Statistical Area 48.1 is controlled both by top down effects (leopard seal predation) and bottom up effects (availability of krill). This pattern does not hold true in Ecospace. When spatial dynamics are considered, the simulation outcomes indicate a sustained decline in fur seals across all fishing effort levels and ice conditions. This result implies that while there may be enough krill in the system to support fur seals, there may not be sufficient overlap between seals and krill to allow for population growth. Indeed, during the later years of the simulations areas of high krill concentration, do not overlap with the South Shetland Islands where fur seals aggregate. It may be that regionally, the decline of krill availability is sufficient to prevent recovery of fur seals even when Leopard seal predation pressure declines. The simulations presented here assume that fur seals do not significantly relocate or shift their breeding colonies, but in the real world such a shift could take place. The on-going Antarctic fur seal surveys conducted by the U.S. AMLR program (Goebel and Reiss 2014) will help shed light on these hypotheses and may detect a shift Antarctic Fur seal colonies.

The fishing levels chosen for this study were meant to illustrate extremes and a middle ground to serve as bench marks for comparing MPA performance (Chapter 4). There is no indication if, or how much, fishing will increase in the future. Both Ecosim scenarios and Ecospace scenarios, indicate that fishing at 12 times the current level, the equivalent of removing the trigger limit and catching 25% of the total allowable catch in

Statistical Subarea 48.1, would likely significantly reduce biomass for all eight monitored species. The CCAMLR has historically been precautionary when setting fishing limits (Miller 1991, Constable et al. 2000, Miller 2002), and the results presented here indicate that it may be beneficial for the CCAMLR to continue its established practice and proceed with caution if there is pressure to increase the catch beyond the trigger limit.

The impact of fishing level is also seen clearly in the spatial distribution patterns of the eight monitored species. As illustrated by krill, there is a greater difference in spatial distribution patterns across fishing levels than across sea-ice conditions. For example, krill aggregate in the southern part of the study area and near the western edge of the Weddell Sea, in the northeastern part of study area. The aggregation is larger and more obvious at lower fishing levels regardless of ice scenario; the aggregation of krill in the southern regions breaks down at the highest fishing level. Observations of krill (Atkinson et al. 2004, Second WS-MPA Domain 1 2015) and sea-ice (Cavalieri et al. 1996, updated yearly) indicate that in real life both concentrate in the southern part of the study area and at the edge of the Weddell Sea. However, the far southern regions experience lower ice conditions more often than the Western Weddell Sea region in the north (Cavalieri et al. 1996, updated yearly), leaving the southern areas more vulnerable to fishing. At the highest fishing level, it is possible that the gravity model (Christensen and Walters 2004) draws enough fishing to the southernmost area during low ice periods that the krill aggregation is disrupted. Ecospace output indicates that at the 12x fishing level, relatively early in the scenario (year 20) when the krill aggregation is present and sea-ice concentrations are low near the southern area of krill concentration, effort is

indeed directed to the southern krill concentration. In later years, after the southern krill concentration has broken up, fishing effort is no longer concentrated in this region. Even though fishing effort is diverted elsewhere, this southern area of krill concentration does not recover and is not evident in Ecospace spatial simulation outcomes for krill in year 60 or year 100 at the 12x fishing level. This result implies that this southern area of krill concentration may be particularly vulnerable to targeted, intense fishing efforts.

While the Ecospace simulations are not directly calibrated, the consistency in results across species and scenarios gives credence to the overall patterns revealed by the model. Namely, that areas of historically high sea-ice concentration maintain their relative importance, and that increasing fishing above the current level can impact both overall trends in biomass accumulation patterns, and spatial patterns of biomass accumulation. This consistency in findings across species and scenarios indicates that a well-designed marine protected area could be effective at slowing population declines.

Summary and Conclusions

Worked progressed in this chapter explored two sea-ice scenarios and four fishing effort scenarios using the calibrated Ecosim simulations. It also created a spatio-temporal model to examine the spatio-temporal impacts on biomass accumulation of these same scenarios. Temporally dynamic Ecosim simulations highlighted the importance of sea-ice conditions in determining population trajectory but indicated that fishing effort level plays a role determining biomass accumulation. Spatio-temporal simulations in Ecospace indicate that when species are allowed to move in response to environmental conditions, fishing effort level has a greater impact on biomass accumulation patterns. Ecosim and

Ecospace simulations further indicated that some species such as Adélie and Chinstrap penguins are unlikely to recover even in the absence of fishing pressure, which is consistent with outcomes from other modelling frameworks (Watters et al. 2013). When only temporal dynamics are considered, the simulation outcomes indicate a temporary increase in Antarctic fur seal biomass. Ecospace simulations do not yield a similar increase, indicating that while there might be enough krill in the system to fuel population growth in fur seals, there may not be sufficient overlap between seals and this important prey item. The scenarios presented here will serve as benchmarks for comparing the efficacy of MPA boundaries. Within the framework of Ecospace, MPA efficacy would be most effectively evaluated by examining its effectiveness at slowing population declines.

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CHAPTER FOUR: EXPLORING MPA OPTIONS WITH ECOSPACE

Introduction

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) has been given the responsibility of managing all marine living resources south of the Antarctic Convergence (McElroy 1984, Nicol and Endo 1999, Constable et al. 2000). The objective of the CAMLR Convention is conservation (Article II, CAMLR Convention, paragraphs 1 and 2), and achievement of this objective is constantly evaluated in the context of many Members' interest in pursuing sustainable fisheries. The CCAMLR has recognized that a number of the Commission's conservation objectives could be met by creating marine protected areas (MPAs) (SC-CAMLR 2005, paragraphs 3.54 i, iii, iv-b and iv-c) Specifically the 2005 MPA workshop affirmed that MPAs are tools that can be used to achieve larger ecosystem and conservation goals (CCAMLR 2005). In 2008, the CCAMLR set establishing a representative system of marine protected areas in the Antarctic as a high priority (CCAMLR 2008, paragraphs 7.3 and 7.4). In 2011 the CCAMLR adopted a framework of objectives to be met by future MPAs approved by the CCAMLR. Many of the objectives relate to conservation values such as, protect a representative sample of biodiversity, promote resilience and serve as a scientific reference area (CCAMLR 2011a).

The CCAMLR began working on developing marine protected areas in earnest with the first MPA workshop in 2005 (CCAMLR 2005, Brooks 2013). The CCAMLR

adopted its first MPA in 2009 (CCAMLR 2009, Brooks 2013) and established MPA planning domains to encourage further MPA planning throughout the Antarctic in 2011 (CCAMLR 2011b, Brooks 2013). The idea for developing a framework to guide future Antarctic MPA design processes was raised during the 2011 MPA workshop (CCAMLR 2011b), and adopted formally later that year as the “General framework for the establishment of the CCAMLR Marine Protected Areas” Conservation Measure (CM) 91-04 (CCAMLR 2011a, Brooks 2013). In addition to requiring that MPA proposals be submitted with boundaries, a management plan, and a research and monitoring plan, CM 91-04 established a broad set of objectives that future MPAs could strive to meet. Included in the list of objectives was protection of a representative sample of biodiversity for the region, preservation of ecosystem process and functions, and maintenance of resilience or the ability to adapt to climate change. It seems unlikely that any one MPA would meet all of these objectives, but the framework provides a broad set of goals to strive for during the planning process. Taken as whole, the MPA goals articulated in this framework imply that the CCAMLR views MPAs mostly as tools to preserve biodiversity, rather than as tools to augment fisheries

Marine Protected Area planners have used several decision support tools to assess biodiversity and draw boundaries sufficient to protect an adequate proportion of each type of biodiversity (Delegation of the United Kingdom 2010, CCAMLR 2011b, Brooks 2013). Past (Brooks 2013). Current MPA planning process underway in the CCAMLR (Second WS-MPA Domain 1 2015, Brooks et al. 2016) have relied heavily on creating static maps of where animals have been sighted and where human activities have

occurred. These maps are then used to maximize protecting biodiversity, while minimizing impact to the fishery and other Antarctic operations. One underlying assumption in processes using static maps is that the ecosystem processes and functions that led to areas of biodiversity concentration in the past would remain spatially stable. This may not be a valid assumption for spatially dynamic ecosystem processes like trophic interactions, or for a dynamic region like the Western Antarctic Peninsula (WAP) region.

In the WAP the sea-ice regime has been shown to be critically important to the spatial structure of the ecosystem, (Ducklow et al. 2007, Ducklow et al. 2013). The WAP has been experiencing dramatic declines in duration and extent of sea-ice (Stammerjohn et al. 2008, Ducklow et al. 2013, Stammerjohn 2013). Already, changes in the patterns of distribution and abundance of several key species such as Antarctic krill (Atkinson et al. 2004) and penguins (Lynch et al. 2012) have been correlated with changes in the sea-ice regime. Therefore, it seems likely that relying solely on static maps to design a protected area for the region may not be sufficient.

Since the adoption of the first MPA in 2009, policy discussions regarding MPAs have been evolving in the CCAMLR. In 2016 the CCAMLR adopted its second MPA, The Ross Sea Region Marine Protected Area with the agreement of CM 91-05 (CCAMLR 2016b). The Ross Sea Region Marine Protected Area was adopted in accordance with the framework laid out in CM 91-04 (CCAMLR 2011a) and had a further stipulation applied to reach consensus from all Members. That stipulation is known as the “sunset clause” (paras 20 and 21) and it limits the period of designation to

35 years, unless consensus is reached to extend the duration, modify the boundaries, or establish a new MPA (CCAMLR 2016b paragraph 20). This provision was necessary to reach political agreement, but runs counter to studies of MPA efficacy which demonstrate that older, longer duration MPAs perform better than newly implemented MPAs (Edgar et al. 2014). Also included in CM 91-05 are requirements for regular reporting of activity conducted within the MPA and regular review to determine if the MPA is meeting its specific objectives (paras. 15-19). These reporting and review requirements are meant to provide information that would assist with adaptive management of the MPA and are consistent with active adaptive MPA management programs that have been effective elsewhere in the world (Gell and Roberts 2003, Gill et al. 2017). The sunset clause requires that the results of the reports and reviews are taken into account when Members decide whether to extend protection beyond 35 years. Members would be free to decide individually if they believe continued protection is merited, and if consensus is not reached protection would end. Establishing a new MPA in the WAP will likely require balancing political needs for a sunset clause with conservation needs for having long-lasting protection.

The Ecospace module of the software package Ecopath with Ecosim allows for spatially and temporally dynamic simulations to be used to assess MPA boundary impact on biomass accumulation patterns (Christensen and Walters 2004). The software can also assess how many years it might take for the impact of the MPA to be noticeable. This decision support tool can therefore be used to investigate which potential boundary

configurations are likely to have the greatest positive impact on biomass accumulation patterns and how long it takes for such impacts to be realized.

The aim of this study is to contribute to the on-going discussions about MPAs in the CCAMLR (Second WS-MPA Domain 1 2015), specifically by looking at boundary configurations that might be of interest to stake holders in the United States, and determining if and when any of the evaluated MPA scenarios would have a positive impact on biomass accumulation patterns.

Methods

Ecospace models the impact of an MPA as a no-take marine reserve, but allows users to specify if the MPA is open to fishing during certain months of the year (Christensen and Walters 2004). For the present study, all evaluated MPAs were modeled as no take reserves that were closed to fishing every month of the year. When an MPA is instated in Ecospace, the software prevents fishing activities (catch and effort) from occurring within the MPA boundaries. MPA scenario evaluation would be most meaningful after an Ecopath model has been successfully created and calibrated in Ecosim (Chapter 2) and after demonstrating that Ecospace was able to adequately represent spatio-temporally dynamic patterns of distribution and abundance (Chapter 3). Additionally, eight 100-year scenarios were developed in Chapter 3 to serve as a benchmarks to compare MPA performance. The eight scenarios examined two different sea-ice conditions (status quo and decreasing ice) and four different fishing levels (none, status quo, 5x, and 12x). The sea-ice scenarios do not represent actual spatially explicit sea-ice

predictions for the region, as those are not available. Rather, the decreasing ice condition represents what might be expected if low ice years, like those experienced between 1996-2012, occurred more frequently. The scenarios also included a cost layer that assigned high cost to areas experiencing greater than 50% sea-ice concentration in future years (Chapter 3), effectively limiting fishing to occur only in low ice conditions where it is much more likely to occur in the real world (Antarctic Ecosystem Research Division Southwest Fisheries Science Center and NOAA Fisheries 2016). The objective of this chapter is to identify four plausible MPA scenarios and evaluate their impact on biomass accumulation patterns compared to each other and to the absence of MPAs. The underlying ecosystem model and scenarios used in this chapter were the same as those described in Chapters 2 and 3, MPA boundary scenarios have merely been layered in as another future conditions permutation.

Developing MPA Boundary Scenarios

The United States (USA) has been an early and active stakeholder in developing Antarctic MPAs (Brooks 2013, Brooks et al. 2016). The USA has a particular interest in developing MPA boundaries in the WAP because United States citizens engage in, and in some cases receive government funding for, a wide range of activities in the region including: long-term multidisciplinary research, management of Antarctic fisheries, consumption of products derived from Antarctic fisheries, and all facets of Antarctic tourism including management of the industry, leading tourism operations, and partaking in tourism operations (Watters 2015). Because of this breadth of interest, the U.S. Delegation to the CCAMLR held a U.S. stakeholder workshop in La Jolla, California in

March of 2015. The aim of the workshop was to identify conservation objectives and areas that U.S. stakeholders are most interested in protecting. Participants were divided into three groups and instructed to identify conservation objectives and then identify areas to prioritize for protection that would seek to meet these objectives. Participants identified a number of protection objectives including (but not limited to): protect krill spawning and larval development, study climate impacts separate from fishing, and preserve integrity of existing studies (Watters 2015). Each of the three groups was given a map of MPA Planning Domain 1, 20 colored squares, scissors, and adhesives. Each colored square represented 5% of the total area of Planning Domain 1. Participants were asked to place the squares, whole or in subsections, on the map to designate the rank order of their protection priorities. The reddest colored squares represented the most important places to protect (top 5%) while the bluest squares represented the areas least important to protect. Participants negotiated priorities and settled upon a consensus prioritization within each group. All three groups' maps were digitized and the prioritization was averaged across groups (Watters 2015) (Figure 41).

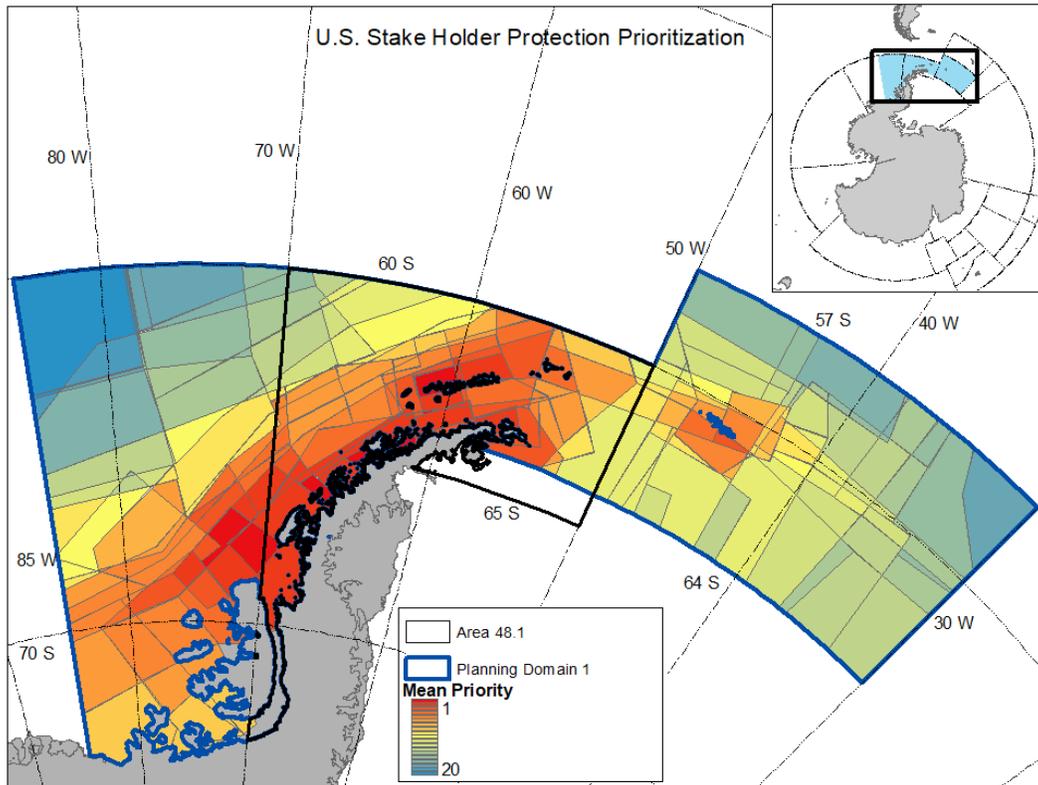


Figure 41 U.S. stakeholder area prioritization

United States stake holders at the La Jolla workshop prioritized continental shelf and near shore areas for protection. There was near unanimous interest in protecting two small canyons near Livingston Island and the Gerlache Strait which were seen as ecologically unique and important (Watters 2015). The Gerlache Strait in particular was thought to function as a nursery area for larval krill (Huntley and Brinton 1991) and as an important foraging area for marine mammals and penguins (Weinstein et al. 2017). These areas also coincided with study areas for many of the stakeholders present, including scientists from the Palmer Long Term Ecological Research (LTER) program and the U.S. NOAA-AMLR program (Watters 2015). The groups' spatial prioritizations were largely

consistent with their stated objectives of protecting areas important to krill and maintaining the integrity of long term ecological research projects.

The highest priority areas also have significant spatial overlap with the krill fishery; protecting the top 15% would displace approximately 50% of the fishery by effort and catch, as documented in the catch logs from 2006-2014 (Watters 2015). Such a significant impact to the fishery could be viewed negatively by the CCAMLR fishing nations and may hinder adoption in the consensus based deliberative body (Brooks 2013). Protecting the top 10% of U.S. priorities would reduce the impact to displacing approximately 40% of fishery effort and catch from 2006-2014 (Watters 2015). A synthesis of global MPA efficacy found that fisheries received the greatest benefit from MPAs when 20%-40% of the current fishery is impacted (Gell and Roberts 2003). Protecting the U.S. stakeholder's top 10% would likely have a fisheries impact similar to the most effective MPAs. However, such a high level of displacement could be viewed negatively by nations wishing to maintain or expand the current level of krill fishing.

The study area used to develop the Ecopath, Ecosim, and Ecospace models, Statistical Subarea 48.1, lies at the Center of Planning Domain 1 and contains most of the highest priority areas for U.S. stakeholders (Figure 41). Two MPA scenarios were developed directly from priorities articulated at the U.S. stakeholder workshop in La Jolla. In the first scenario, the La Jolla participants top 5% areas (LJ5) that lie within Statistical Subarea 48.1 were set aside as a no-take marine reserve. This action would displace approximately 12% of fishery catch and effort as reported for the years 2006-2014 (Watters 2015). In the second scenario, all parts of the La Jolla participants' top

10% areas (LJ10) that are within Statistical Subareas 48.1 were set aside as a no take marine reserve and would displace approximately 40% of fishery catch and effort for the years 2006-2014 (Watters 2015).

MPA size and connectivity have also been shown to impact efficacy (Gell and Roberts 2003, Gaines et al. 2010, Ban et al. 2017, Gill et al. 2017). Past experience in the CCAMLR has shown that MPAs that have minimal spatial overlap with the fishery are adopted more readily, even if they are quite large (Brooks et al. 2016). With these two points in mind, two additional MPA scenarios were developed that would include some of the areas with highest priority for U.S. stakeholders at the La Jolla workshop, would have a larger more contiguous area compared to protecting the entirety of the top 5%, and would have minimal spatial overlap with fishery. The CCAMLR has divided Statistical Subarea 48.1 into Small Scale Management Units (SSMUs) to help spatially stratify krill catch (Constable and Nicol 2002, Constable 2011). The boundaries of the SSMUs are well known by the CCAMLR Members, and are used when reporting krill catches (CCAMLR 2017). The Antarctic Peninsula Pelagic Area (APPA) is the largest SSMU in Statistical area 48.1. The APPA SSMU experiences very low fishing pressure, accounting for less than 1% of the krill fishing effort and catch from 2006-2014. (CCAMLR 2017). The southern portion of the LJ10 scenario is contained entirely within the APPA SSMU, and this southern portion of the LJ10 overlaps with approximately one third of the LJ5 scenario. The southern portion of the LJ10 scenario (LJ10S), was considered as the third MPA scenario. The fourth MPA scenario set aside an entire SSMU, the Antarctic Peninsula West SSMU (APW) as an MPA. Because SSMUs were specifically established to spatially

manage the krill fishery (Constable and Nicol 2002, Constable 2011), the CCAMLR might be interested in designating an existing management unit as an MPA. During the years 2006-2014, approximately 8% of the fishing effort and catch were contained in the APW SSMU (CCAMLR 2017). Additionally, the boundaries of this SSMU overlap with portions of the top 5% and top 10% priority areas of La Jolla workshop participants (Figure 42).

In Statistical Subarea 48.1 krill are the main prey item for a number of predators and also support the only commercial fishery in the region (CCAMLR 2017). Therefore, it would be important to consider how the MPA boundaries would overlap with the areas of greatest importance to krill. Figure 42 illustrates the location of each of the four MPA scenarios in relation to the Ecospace simulation outcomes for krill biomass accumulation at the end of the calibrated data (i.e for the last time step for which field observations were used to calibrate the Ecosim simulations and judge Ecospace performance, December 2012, the end of year 17 in the simulation). The LJ10 and LJ10S scenarios had the greatest overlap with Ecospace indicated areas of greatest krill relative biomass and APW had the least overlap with Ecospace indicated areas of greatest krill biomass (Figure 42).

All four MPA scenarios were run as Ecospace simulations using all eight combinations of sea-ice scenario and fishing level (as described in Chapter 3). These scenarios reflect MPA configurations that might be helpful in learning about how MPA boundaries could interact with ecosystem dynamics in the WAP. The scenarios were chosen to highlight areas that might be of interest to U.S. stakeholders, but they do not represent MPA proposals or even less formal MPA scenarios under consideration by any

Delegation to the CCAMLR. The scenarios put forward here are simply part of an academic exercise that can hopefully contribute to the on-going discussion regarding Antarctic Peninsula region MPAs in the CCAMLR.

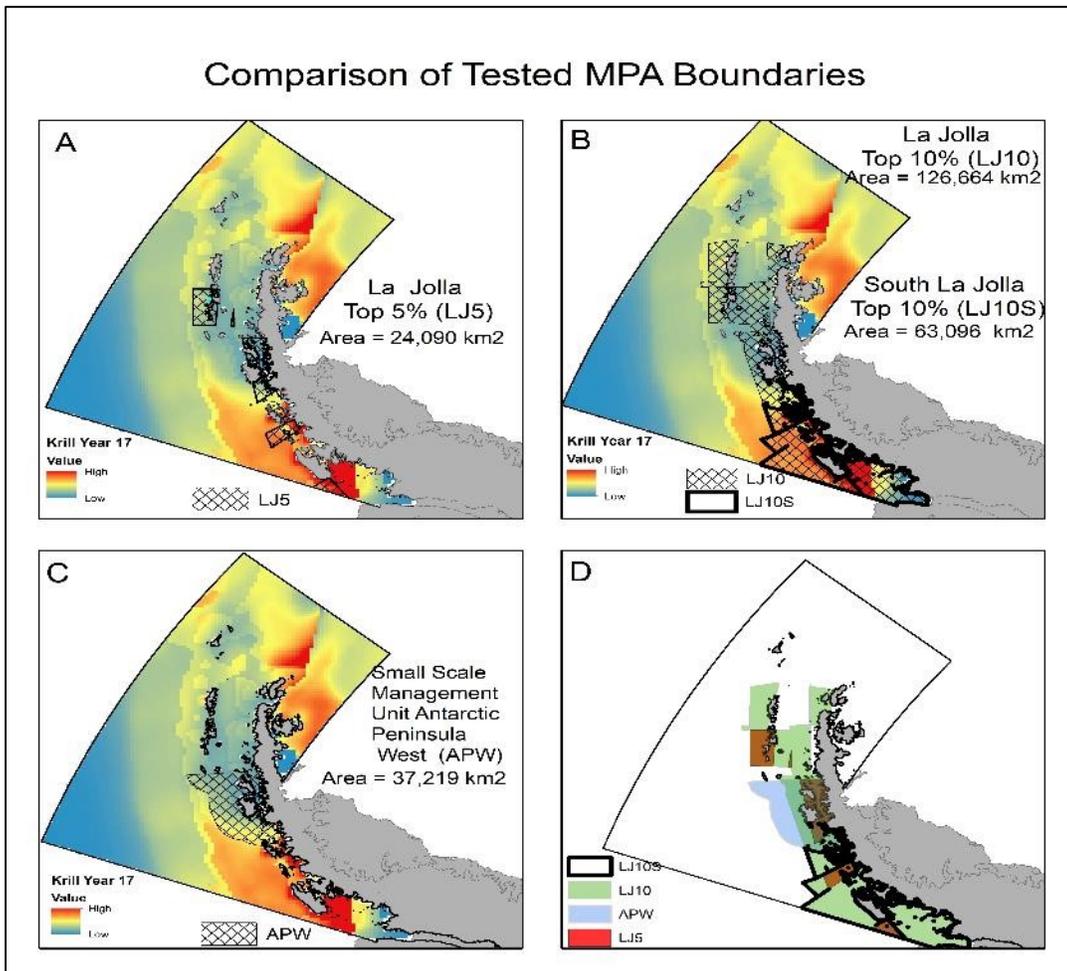


Figure 42. Maps of evaluated MPA scenarios. Locations of LJ5(A), LJ10 and LJ10S (B) and APW (C) MPA scenarios in relationship to areas where Ecospace outcomes indicate krill aggregate and in relation to each other (D). All areas in LJ 5 scenario are included in LJ10 scenario. All areas in LJ10S scenario are included in LJ10. Scenario. The krill map used is from the Ecospace spatial outcome for December 2012, the last time step for which the Ecosim data were calibrated and Ecospace scenario was considered for adequacy.

Results

For each of the four MPA scenarios, the model was run through all eight combinations of ice scenario (status quo and decreasing) and fishing level (none, status quo, 5x, and 12x). Simulation outcomes for relative biomass and MPA performance were compared across conditions. The presentation of results focusses on the eight monitored species used to calibrate the Ecosim simulations and to judge the adequacy of the Ecospace base scenario (Chapters 2 and 3). Due to the calibration and tuning process, model performance was likely highest for these eight species. Additionally, these species represent indicator species that the CCAMLR has used to assess whole ecosystem health (Agnew 1997).

Similar to the trials run in Chapter 3, fishing level had a significant impact on simulation outcomes. When an MPA had an impact, that impact was greatest at the twelve times fishing level. This is illustrated for Adélie penguins in Figure 43. With the exception of *G. gibberifrons*, all of the eight monitored species showed some positive impact from at least one MPA scenario at the 12x fishing level. Consistent with the findings of Chapter 3, no scenarios, including the total cessation of fishing, resulted in simulation outcomes for already declining species to return their 1996 levels. This is illustrated below in decreasing ice conditions for Adélie penguins (Figure 43) and holds true for Antarctic fur seals, chinstrap penguins, *G. gibberifrons*, and krill in both decreasing and status quo ice conditions. In the graphs, log relative biomass values greater than zero represent an increase over initial biomass. Increases were only indicated for the three species that were increasing during the calibration period: Gentoo penguins, *C. gunnarii*, and *N. rossii*.

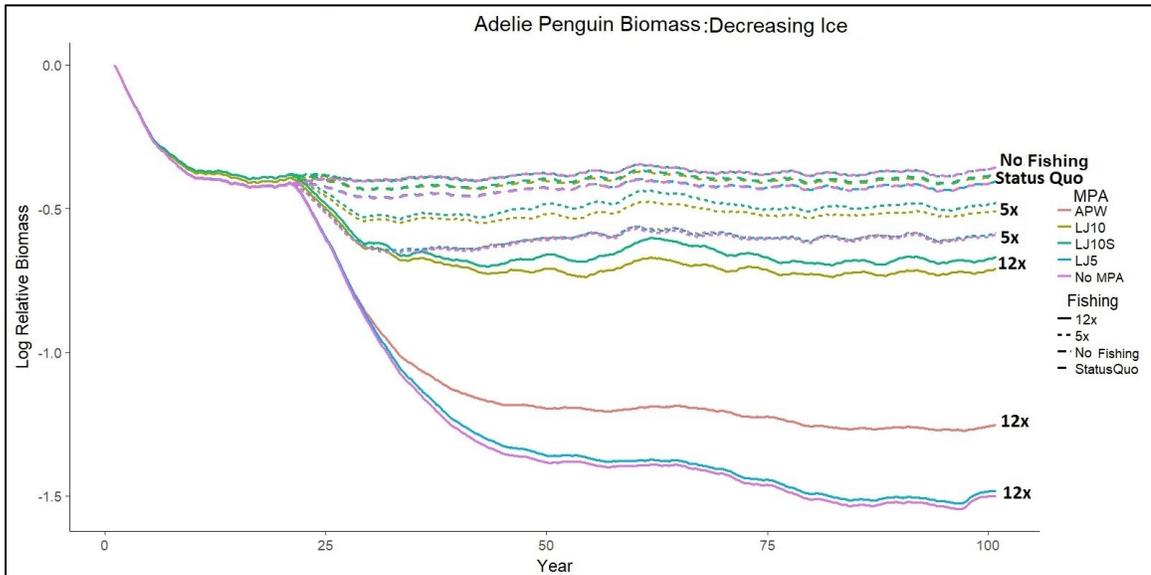


Figure 43. MPA impact on Adélie Penguins in decreasing ice conditions. Log relative biomass simulation outcomes reflect changes in biomass compared to the starting 1996 biomass (0.0). No MPA scenarios, or even the complete end of fishing, cause the model to indicate returning to biomass as high as the starting biomass. Note that at the “No Fishing” level simulation outcomes are indistinguishable across MPA Scenarios. At the “Status Quo” fishing level, the LJ10 and LJ10S simulation outcomes separate out from all other MPA scenarios, but are indistinguishable from each other. At the “5x” fishing level, LJ10S simulation outcomes are slightly higher than LJ10 simulation outcomes and simulation outcomes under all other MPA scenarios are indistinguishable from each other. At the 12x fishing level, simulation outcomes clearly separate out by MPA scenario.

Sea-ice condition minimally impacted simulation outcomes for relative biomass and MPA performance. This is true for species that react positively to increasing sea-ice conditions, like Adélie penguins, or species that react positively to increasing open water conditions like Gentoo penguin. Figure 44 illustrates this at the 12x fishing level, where MPA impact is greatest and easiest to see. While ice conditions do impact relative biomass simulation outcomes and MPA performance, fishing level (Figure 43), and MPA scenario (Figure 44) appear to have a larger impact on biomass accumulation patterns. Because decreasing sea-ice conditions are more likely to occur in the future, only

simulation outcomes for the decreasing ice condition are further included in this chapter. Simulations outcomes produced under status quo ice conditions exhibit similar patterns and are presented in Appendix 6.

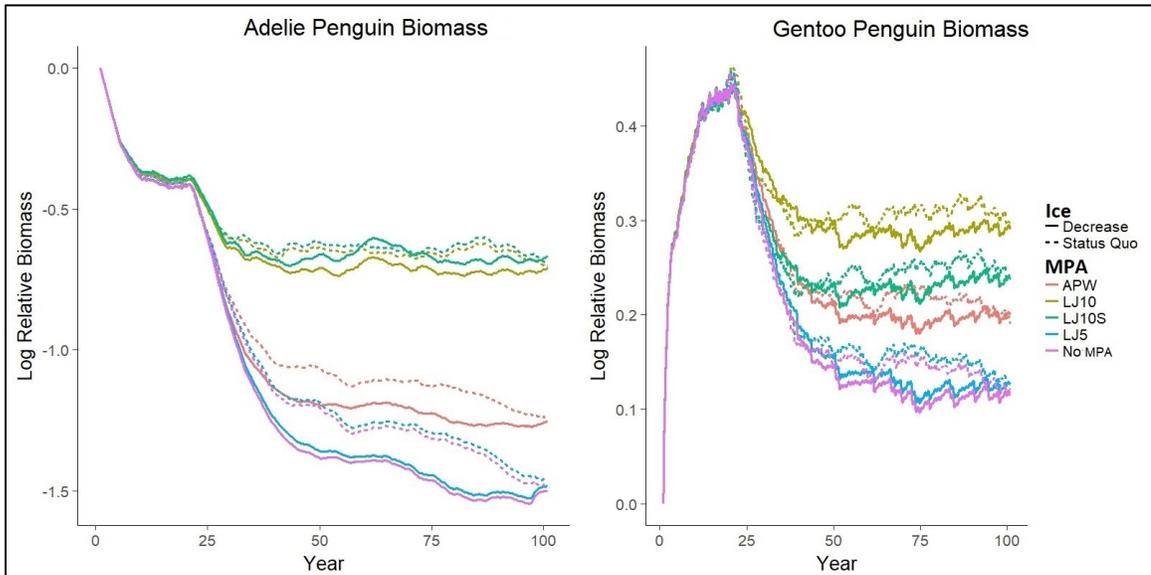


Figure 44. Comparison of MPA impact across ice conditions under 12x fishing. MPA scenario has the larger impact on simulation outcomes for relative biomass; Sea-ice condition merely stratifies simulation outcomes within the scenario

The 12x fishing level serves as a worst-case scenario, where the CCAMLR simply removes the trigger limit (CCAMLR 2010) and allows fishers to catch 25% of the total allowable catch in Statistical Subarea 48.1 (CCAMLR 2016a). It also serves as a convenient bench mark to judge if an MPA scenario would be likely to have any impact. At the 12x fishing level, MPA impact was stratified by size. The two largest scenarios, LJ10 and LJ10s, had the largest impact, followed by APW, and then the smallest scenario LJ5. However, in the near-term fishing levels are more likely to remain near the current level or have a moderate increase. Therefore, it would likely be more immediately informative to examine MPA impacts at the status quo or 5x fishing levels.

At the status quo fishing level, only the LJ10 and LJ10S MPAs had noticeable positive impacts on species that were declining. Adélie penguins, Antarctic fur seals and krill all showed slight increases in relative log biomass outcomes in the LJ10 and LJ10S scenarios compared to the no MPA condition. These impacts became noticeable at approximately 15 years into the simulation, with greatest impacts emerging at about 25 years. The LJ10S scenario had a slightly more positive impact on these species than the LJ10 scenario (Figure 45 panels A, B and H). At the 5x fishing level (Figure 46), the LJ10 and LJ 5 scenarios slightly positively impact Chinstrap penguins (Figure 46 C). The LJ10 S scenario had a negative impact on Gentoo penguins and *C. gunnarii*, which were indicated to increase regardless of conditions (Figure 46 D and E).

At both the status quo and 5x fishing level, simulation outcomes indicated that MPA scenario impacted the spatial distribution patterns of Antarctic krill, Antarctic fur seals and Adélie penguins. The impact of the MPA scenario was greater at the 5x fishing level. Biomass concentrated in the southern portion of the LJ10 scenario and in the LJ10S scenario as compared to the same area under all other MPA scenarios (Figure 47 and Figure 48). No other MPA scenario produced a similar result. In effect, the LJ10 and LJ10s scenario enhanced the concentration of krill in that region. Status quo ice conditions and the spatial results for the remaining seven species have been provided in Appendix 7. It may be that this enhanced concentration of krill is what drives the increases experienced by two krill predators under the LJ10 and LJ10S scenarios: Antarctic fur seals and Adélie penguins.

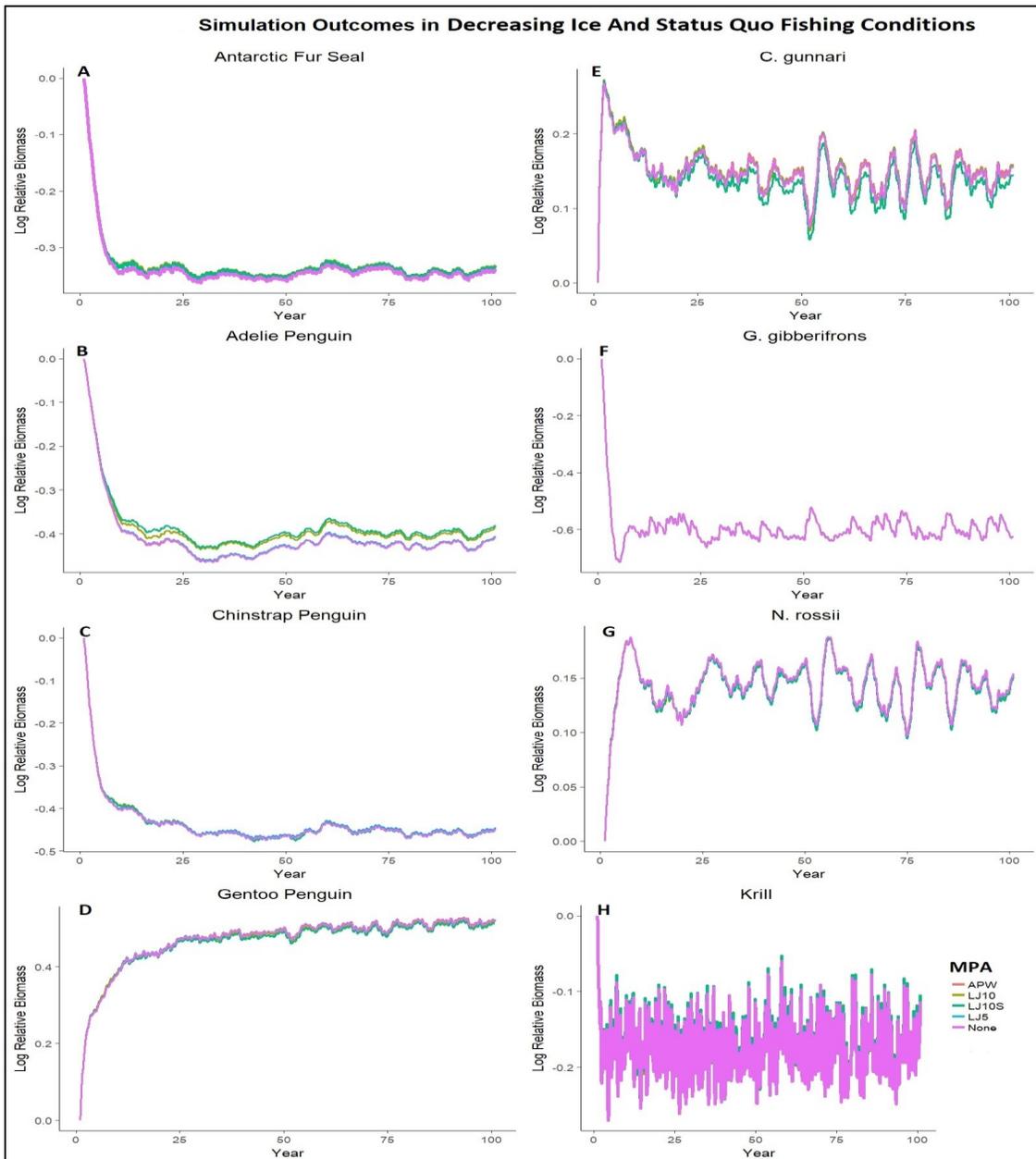


Figure 45. Comparison of MPA impact at status quo fishing levels. The LJ10 MPA scenario results in slightly higher relative biomass outcomes for Antarctic fur seals (A), Adélie Penguins (B) and Krill (H). Chinstrap penguins (C), Gentoo penguin (D), *C. gunnari* (E), *G. gibberifrons* (F) and *N. rossii* (G) were not impacted by any MPA scenarios under status quo fishing conditions. Please note the the plot order is the reverse of the list of MPA scenarios. That is, “No MPA” plots on top and APW plots on bottom. If a line for an MPA is not visible, its plot was similar enough to leave it obscured.

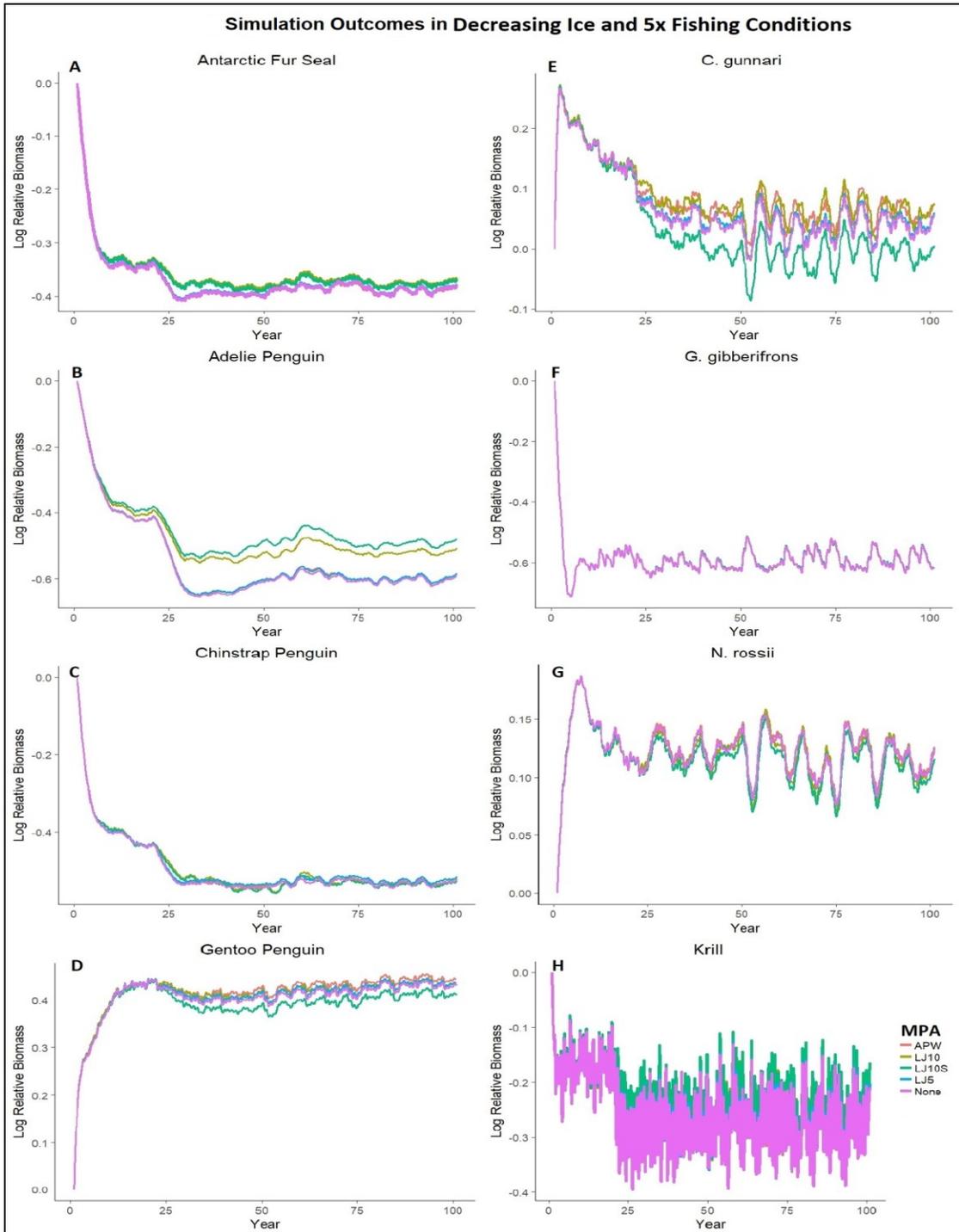


Figure 46. Comparison of MPA impact at 5x fishing level. The LJ10 and LJ10S MPA scenarios result in slightly higher relative biomass simulation outcomes for Antarctic fur seals (A), Adélie Penguins (B) and Krill (H)

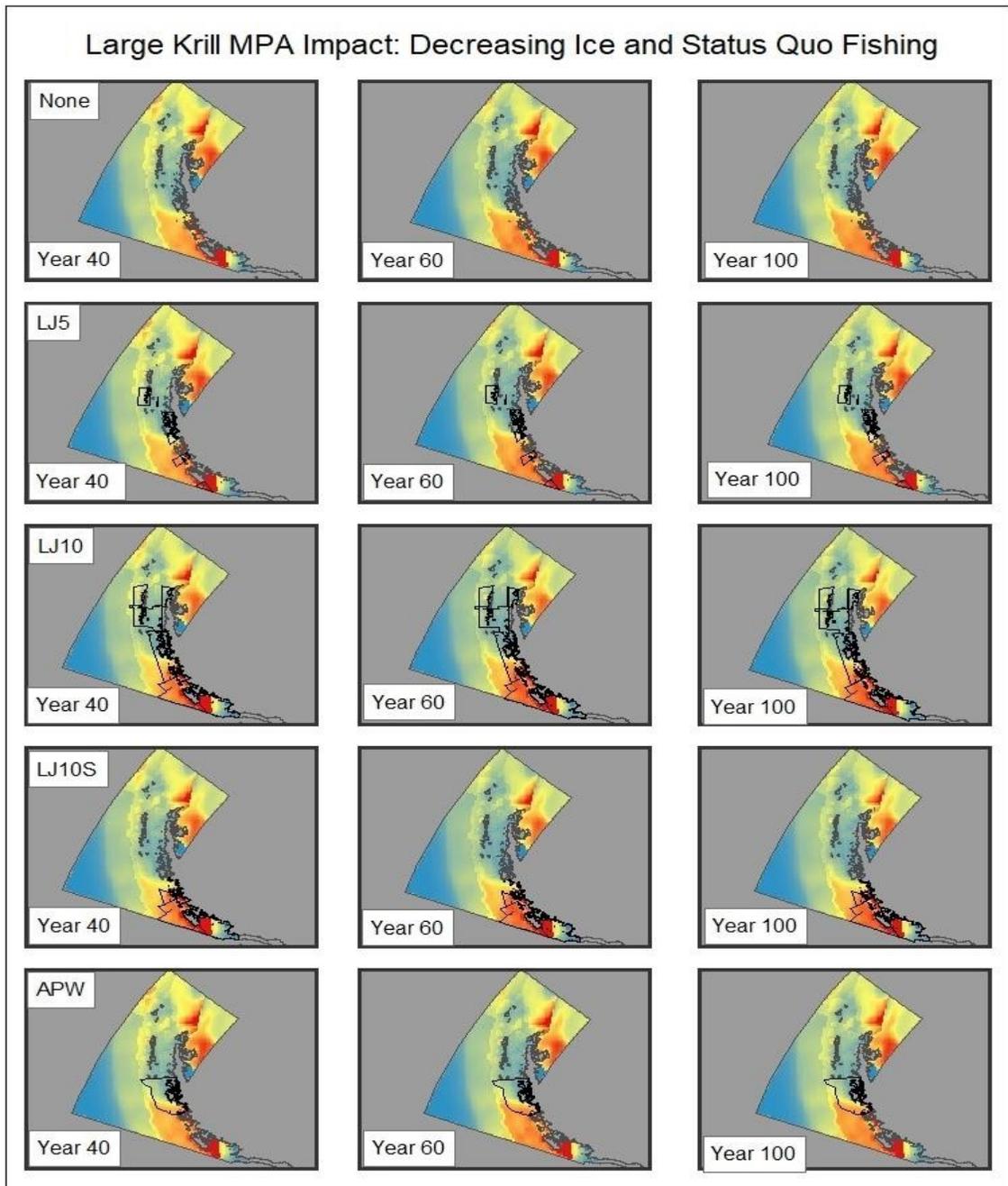


Figure 47. MPA impact on Large Krill biomass under status quo fishing pressure. Red color indicates areas of greater concentration. Krill concentrate in the southern part of the LJ10 and in the LJ10S MPA scenarios.

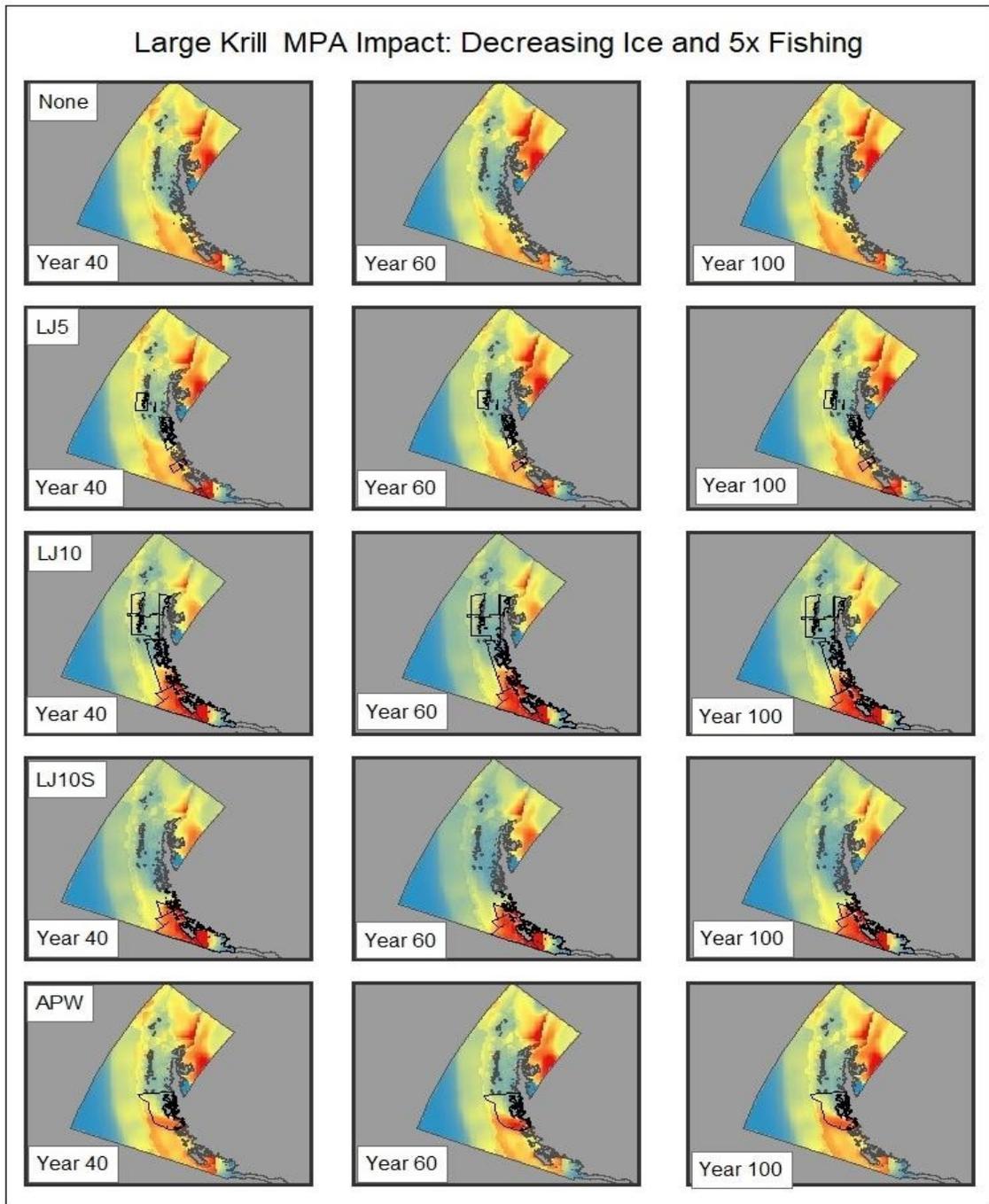


Figure 48. MPA Impact on Large Krill biomass under 5x fishing pressure. Red color indicates areas of greater concentration. Krill concentrate in the southern part of the LJ10 and in the LJ10S MPA scenarios.

The impacts of the MPA scenarios on the fishery were examined in two ways. In the first spatial location of fishing effort was compared across the different MPA scenarios (**Error! Reference source not found.** and **Error! Reference source not found.**). The spatial pattern of fishing effort was noticeably altered by both the LJ10 and LJ10S scenarios while the LJ5 and APW scenarios had little impact. The LJ10 and LJ10S scenario displaced fishers from the southern area of krill concentration, shifting fishing effort into the more northern part of the study area and the Western Weddell Sea earlier in the simulation runs. The larger LJ10 scenario displaced slightly more fishing than the LJ10S scenario, and as a result fishing is slightly more concentrated in the Western Weddell Sea than in the LJ10S scenario. By year 100 in the simulation runs, the spatial distribution of fishing is similar across MPA scenarios; there are two areas of fishing effort concentration, one in the western Weddell Sea and a second area of fishing concentration near the area of southern krill concentration. The location of this southern area of fishing effort concentration is influenced by MPA scenario. The intensity of concentration in the Weddell Sea is also influenced by MPA scenario, with greatest effort in the Weddell Sea indicated under the LJ10 scenario.

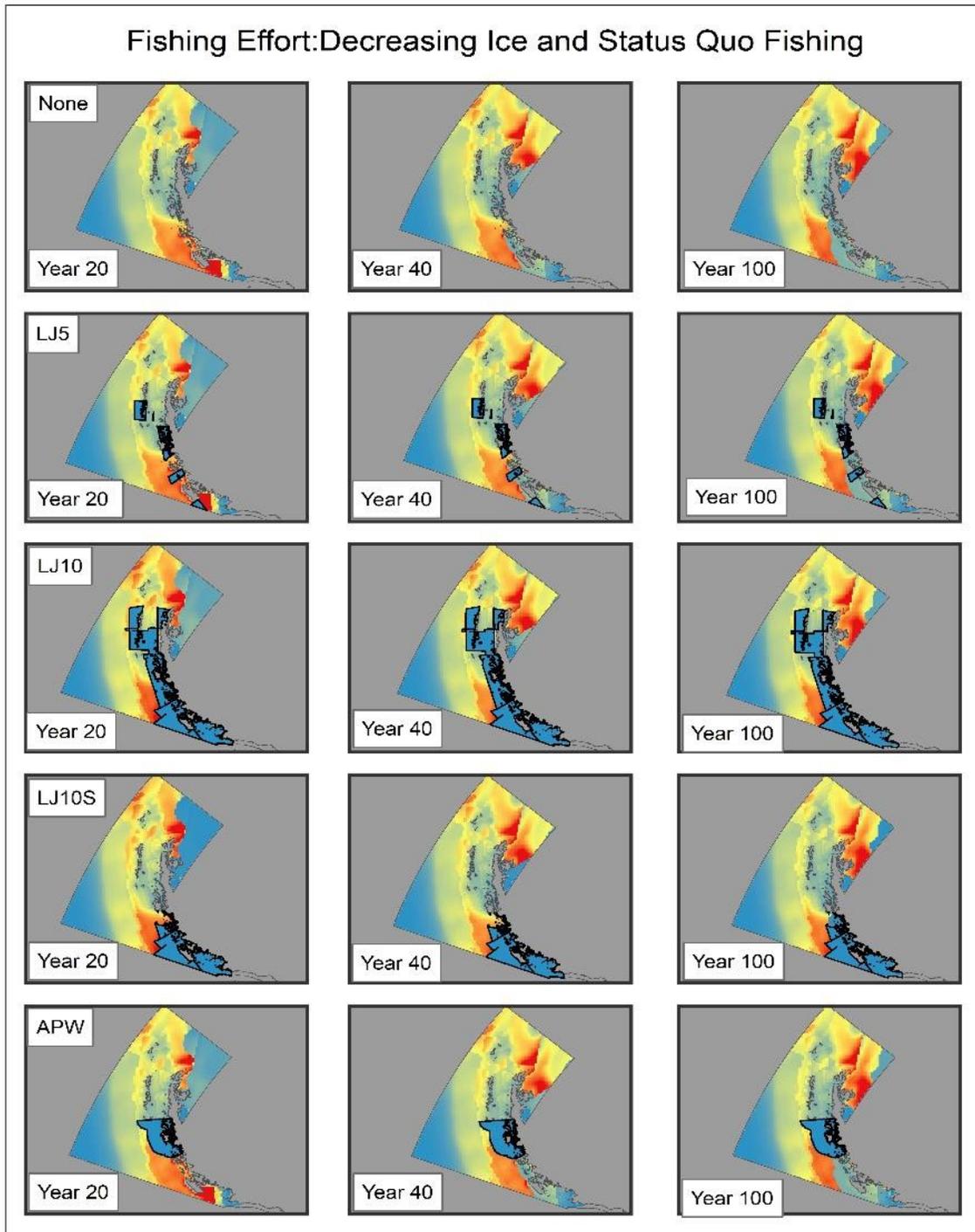


Figure 49. Location of fishing effort in decreasing ice and status quo fishing conditions across MPA scenarios. Redder color indicates more fishing effort.

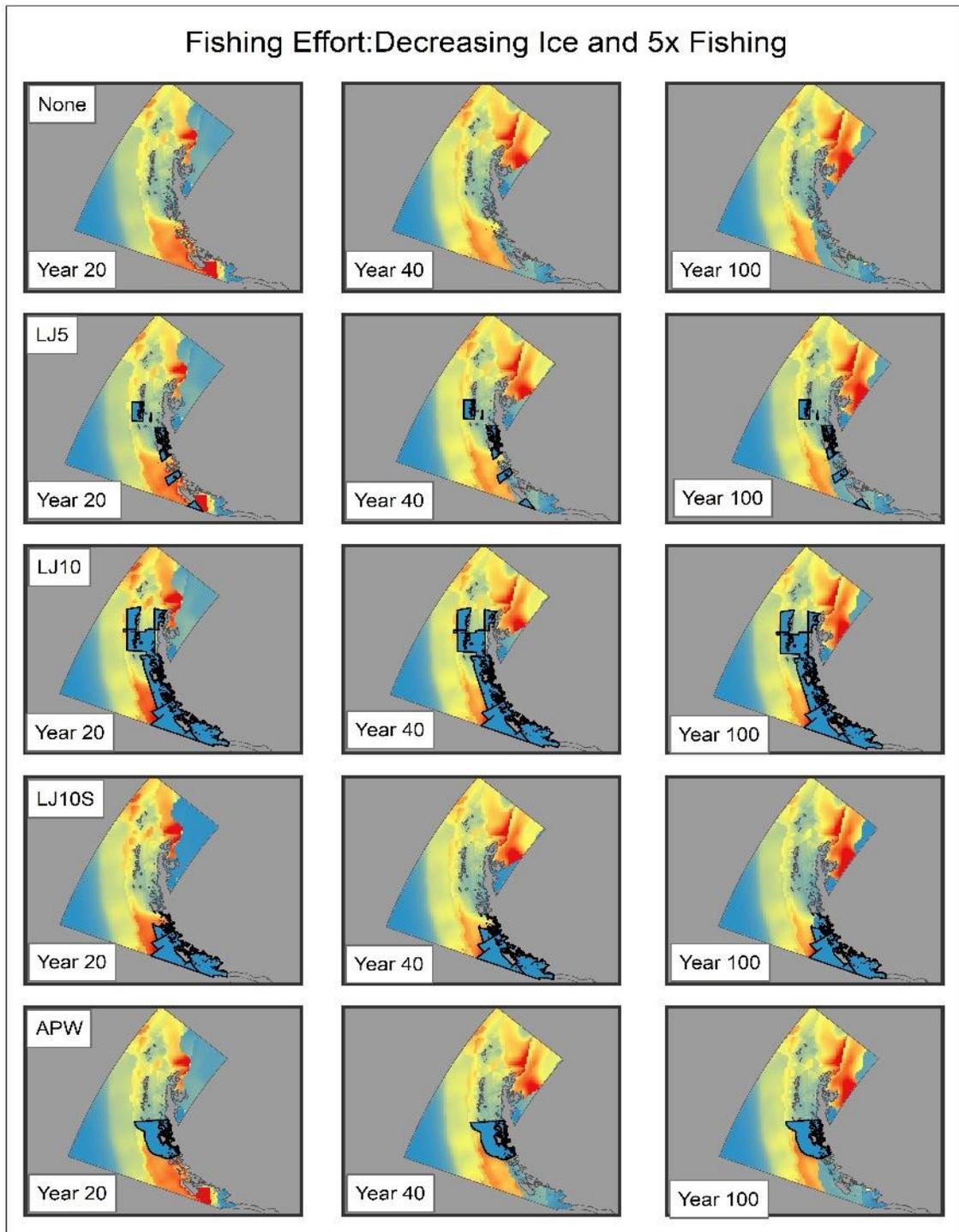


Figure 50. Location of fishing effort in decreasing ice and 5x fishing conditions across MPA scenarios. Redder color indicates more fishing effort.

The second way to examine MPA impacts was to compare the simulation outcomes for krill catch at the end of the simulation under decreasing sea-ice conditions at the status quo and 5x fishing levels to the simulation outcomes for landings under the same conditions when no MPA scenario was in place (Figure 51). The LJ10 and LJ10S scenarios had the largest impact, with simulation outcomes indicating catch decreasing by approximately 10-14%. This value is very different than what would be expected if spatial overlap with the fishery from 2006-2014 were used to judge potential impact. Approximately 40% of the fishery catch and effort from that period overlaps with the LJ10 scenario (Watters 2015) and less than 1% overlaps with the LJ10S scenario (CCAMLR 2017). For completeness, catch comparisons in the status quo ice scenario and at the 12x level are presented in Appendix 8. At this high catch level, presence of any MPA actually increases catches.

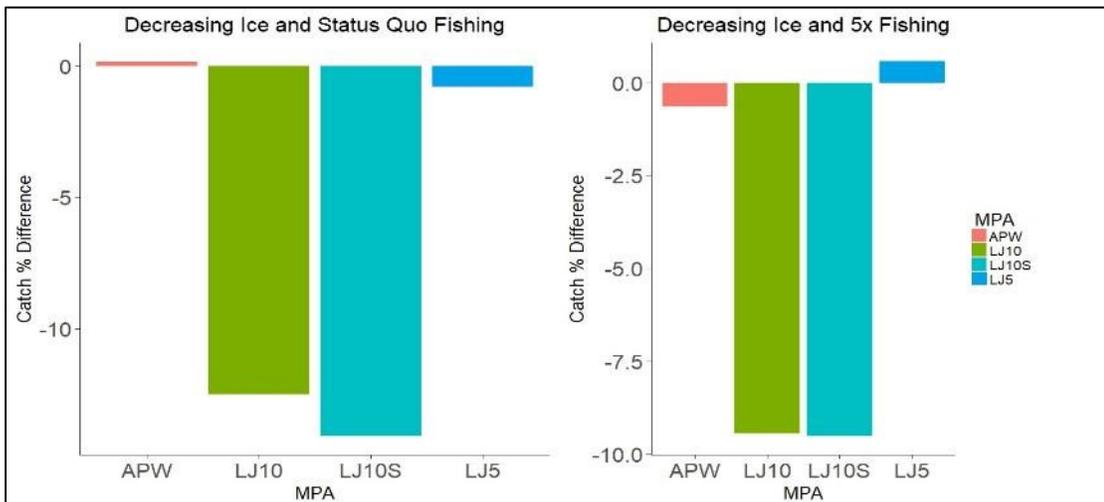


Figure 51 MPA impact on krill landings. The landings percent difference reflects the difference in catch at year 100 for the MPA scenario compared to the catch in the same fishing and ice conditions with no MPA in place.

Discussion

The simulations suggest that a well-designed MPA could be effective at slowing biomass declines for some species under a variety of conditions. Simulation outcomes indicated that Antarctic fur seals, Adélie penguins, and krill would have higher relative biomasses when the LJ10 and LJ10S MPA scenarios were in place, under both decreasing and status quo ice conditions. At higher fishing levels, impacts from MPAs were more evident and included a slight positive impact on chinstrap penguins. In general, these simulations indicate that establishing a sufficiently large and appropriately located MPA in the WAP region could mitigate the effects of sea-ice loss. A large and well-located MPA could thus promote resilience to the impacts of climate change.

Size was an important factor in determining MPA impact on biomass accumulation patterns. This may be best illustrated at the 12x fishing level where all MPA scenarios had a positive impact on Adélie penguin relative biomass. This impact was stratified by MPA size. The two largest MPA scenarios (LJ10 and LJ10S) had the largest impact, followed by the APW MPA scenario, and the smallest MPA scenario (LJ5) had the smallest impact.

Location also impacted MPA effectiveness and interacted with size. In the southern part of Statistical Area 48.1, the LJ10, LJ10S, and LJ5 scenarios have a high degree of overlap with each other and with the area where the simulations indicate krill will concentrate. Comparing these three scenarios, the impact does not stratify by total MPA size. The LJ10 scenario is twice the size of the LJ10S scenario, but the LJ10S scenario has a comparable or slightly larger positive impact on Antarctic fur seals, Adélie penguins and krill. The LJ10 and LJ10s scenarios have the same large overlap with the

area where simulations indicated that krill would concentrate, while the LJ5 scenario includes much less of this area. Therefore, it may not be the total size of the MPA that matters, but rather the amount of high quality habitat protected that determines MPA impact. The slightly more positive impact of the LJ10S scenario might be explained by the pattern of fishing displacement. The LJ10 scenario displaces slightly more fishing than LJ10S, and as a result fishing becomes slightly more concentrated in the western Weddell Sea under the LJ10 scenario. This slight increase of fishing concentration in the Weddell sea might be enough to reduce MPA performance compared to the LJ10S scenario

When comparing MPA scenarios that overlap in the region just north of the area of krill concentration (LJ5, LJ10, and APW), size appears to be more important than the existence of overlap with the area of krill concentration. The larger APW MPA outperforms the smaller LJ5 MPA. The LJ5 MPA overlaps with the area of krill concentration, while the APW MPA does not. Further, under the LJ5 scenario the spatial distribution of fishing effort was only impacted early in the scenario. By year 40, there was no noticeable differences in the spatial distribution of fishing effort between the LJ5 scenario have no MPA. Whereas the APW scenario displaced some fishing effort for the duration of the simulation. This implies that the amount of high quality habitat protected by the LJ5 scenario is not sufficient to overcome the large size difference between the two scenarios.

The southern area of krill concentration, seems to be influential in determining MPA impact. This effect increases under decreasing ice conditions and higher fishing

pressure. This may be related to the implementation of the fishing gravity model in Ecospace. Fishers in the simulations are pulled towards areas of high concentration of their target species and low cost, and are excluded from areas designated as an MPA (Christensen and Walters 2004). The cost layer used to inform fishers' behavior for the future scenarios assigned a high cost to areas that experienced greater than 50% sea-ice concentration (Chapter 3). In low ice years the southern area where krill concentrates often experiences sea-ice concentration less than 50% (Cavalieri et al. 1996, updated yearly) and would be available to the fishery (Antarctic Ecosystem Research Division Southwest Fisheries Science Center and NOAA Fisheries 2016). At higher fishing levels, the fishing pressure may be sufficient to disrupt the concentration of krill. The LJ10 and LJ10S scenarios may effectively act as buffers and improve resiliency by excluding fishers from the important and vulnerable southern area of krill concentration. Under these scenarios where no fishing effort is directed into the southern area of krill concentration, the krill concentration grows and intensifies over the course of the simulations.

The finding that both size and location of MPA determine impact is consistent with the broader literature which has found that MPAs must cover a sufficiently large portion of ecologically important areas to offer meaningful protection (Gell and Roberts 2003, Gaines et al. 2010, Gill et al. 2017). The size needed to be effective likely reflects local conditions in spatial ecology. While the LJ5 scenario is an area of importance to krill and to U.S. stakeholders, it may not be large enough to offer meaningful protection and achieve U.S. stakeholders' objectives. The LJ5 scenario, as compared to MPAs

elsewhere in the world, is not a small MPA. MPAs larger than 10,000 km² are considered large scale and particularly effective (Ban et al. 2017). At 24,090 km², the LJ5 scenario is nearly two and a half times the size of some large, effective MPAs. The APW scenario, which does not overlap with the area where krill concentrates, is 50% larger than the LJ5 scenario and has a larger impact. This suggests that to be effective in the WAP an MPA might need to be much larger than elsewhere in the world to cover the spatial ecology of this krill centric ecosystem.

When an MPA scenario had a positive impact on biomass accumulation patterns, it took more than a dozen years for this impact to be noticeable, and the largest gains weren't realized until approximately 25 years into the simulation. This has significant implications when considering a "Sunset Clause", as described in the Conservation Measure (CM) 91-05 which established the Ross Sea region MPA (CCAMLR 2016b). This CM also requires regular monitoring of MPA performance and requires unanimous consent to renew the MPA after it has been in force for 35 years (paragraph 20). It is reasonable to assume that similar conditions will be imposed if an MPA is agreed in the WAP. Therefore, it may be more productive to set MPA goals and objectives that are readily measurable and achievable within the sunset clause period. Such a stipulation might favor agreement on MPA goals focus on representativeness, or how much of each type of biodiversity the MPA protects (Pressey et al. 1993). Such goals are easily measured at all stages of MPA design and implementation.

The simulations conducted here suggest that MPAs can be effective at slowing population declines and that impacts are noticeable in a shorter time period than the 35

years set by the Ross Sea Region MPA sunset clause. It may be productive to set MPA goals in terms of incrementally decreasing the current rate of decline. Setting such goals would raise several practical issues that would need to be resolved. Explicit measurable goals for slowing the rate of decline would need to be agreed. Consideration could also be given to how quickly impacts could be measured. Additionally, a monitoring strategy would need to be developed that had high enough frequency and precision to detect the desired rate of change. This may require additional surveys beyond what is already routinely conducted in the region. It might be helpful to consider the frequency, intensity, and continued funding of monitoring efforts when setting goals for any eventual MPA.

In addition to a proposed MPA's ability to meet conservation goals, the CCAMLR would also consider the MPA's potential impact on the fishery. The CCAMLR has typically considered fisheries impact in terms of spatial displacement (Watters 2015). If a proposed MPA displaces a significant amount of contemporary fishing, it could be challenging for that MPA to be adopted (Brooks 2013). As an example, the LJ10 scenario is inline with many of the objectives laid out in the General framework for the establishment of CCAMLR Marine Protected Areas (CCAMLR 2011a), and this modeling study indicates it would have positive impacts on the biomass accumulations of three currently declining species. Yet if the CCAMLR considers spatial displacement of the current fishery, rather than impact on future catches indicated by Ecospace simulation outcomes, this scenario may be deemed to have an unacceptably large impact (Brooks 2013) of displacing 40% of the current krill fishery (Watters 2015). In recent years krill fishers have moved from fishing large parts of the Antarctic and

Statistical Subarea 48.1, to voluntarily restricting their fishing areas to those they feel are most productive (Nicol and Endo 1999, Kawaguchi and Nicol 2007). In recent MPA design processes fishing nations have fought to preserve access to fishing grounds (Brooks 2013, Brooks et al. 2016). They may be more likely to consent to an MPA similar to the LJ10S scenario which would displace less than 1% of the current fishery (CCAMLR 2017) and have the same positive impact on biomass accumulation patterns as the LJ10 scenario. However, if Members consider that the future fishery may want to expand south to utilize the southern area of krill concentration, spatial overlap with the current fishery may not be the most reliable measure to judge if an MPA scenario might be politically palatable.

Ecospace analyses of landings indicate that the geographical overlap with the current fishery may not be the best proxy for estimating MPA impact on catch. Despite large differences in spatial overlap with the current fishery, simulation outcomes indicated that both the LJ10 and the LJ10S scenarios would decrease landings by approximately 10-14% compared to simulations run under the same conditions with no MPA in place. A 10-14% impact on fishery could be more acceptable to fishing nations than the 40% impact predicted by contemporary displacement under the LJ10 scenario. It is likely that the true impact of the LJ10 scenario lies somewhere between these estimates. In Ecospace, the gravity model efficiently pulls fishers towards areas with a high concentration of the target species concentrations and low cost (Christensen and Walters 2004). In the current simulations, costs for future years were based solely on input sea-ice concentration and do not account for fishers' tendency to visit spatially

constrained preferred fishing grounds (Nicol and Endo 1999, Kawaguchi and Nicol 2007). In the simulations, fishers efficiently visit areas that have both high krill concentration and low sea-ice concentration, even when these conditions occur in places that have not been fished recently. In the real world, fishers may not be as efficient. It can take years or decades for them to identify consistently good fishing grounds, that they will preferentially target (Nicol and Endo 1999, Kawaguchi and Nicol 2007). This process of looking for new fishing grounds would likely skew the impact towards an estimate derived from spatial displacement, until fishermen establish new preferred fishing grounds. Because the far southern region protected by the LJ10S scenario is of little current interest to fishers and Ecospace simulation outcomes indicate modest impact to future catches, it may be possible to secure sufficient political support to include this region in future MPA proposals.

The LJ10 and LJ10S scenarios emerge as the best evaluated scenarios. They both significantly increased relative biomass simulation outcomes for three monitored species that are currently in decline or predicted to decline as a function of climate change: Antarctic fur seals (Goebel and Reiss 2014), Adélie Penguins (Lynch et al. 2012) and krill (Atkinson et al. 2004, Reiss et al. 2017). All evaluated MPA scenarios fell short on positively impacting the other two monitored species which are known to be declining: chinstrap penguins (Lynch et al. 2012) and *G. gibberifrons* (Kock and Jones 2005, Kock and Jones 2012). The LJ10S scenario may be the most politically palatable option because it has very little spatial overlap with the contemporary krill fishery, but it is unclear whether southern areas rich in krill may become of interest to fishers.

The scenarios investigated here were designed to learn about how an MPA could function in the WAP, and specifically to include some areas that might be of interest to U.S. stakeholders. While the simulations yielded some promising results, none of the scenarios as presented here would be appropriate to advance in their current state as MPA proposals. As an example, the LJ10S scenario, which would spatially displace less than 1% of the current fishery, is not likely an appropriate standalone MPA. The LJ10S scenario falls short of meeting some of the objectives laid out in the General framework for the establishment of CCAMLR Marine Protected Areas (CCAMLR 2011a). Specifically, it is located so far south that it may be deemed not to contain a representative sample of habitat (CCAMLR 2011a paragraph 2i). Some species of conservation importance such as the currently declining *G. gibberifrons* occur in the northern part of the study area (Iwami and Kock 1990, Kock and Jones 2005), and none of their known habitat is included in the LJ10S scenario. The LJ10S scenario also fails to protect key life history stages (CCAMLR 2011a paragraph 2ii) of species of conservation interest such as the breeding colonies of Antarctic fur seals, which are currently confined to the South Shetland Islands (Second WS-MPA Domain 1 2015). The LJ10S scenario might offer some meaningful protection if species shift their distribution south in response to climate change. However, such shifts in distribution were not investigated in the current study, and it is unclear if such a significant shift to the south would even be likely. The far south location of the LJ10S scenario means that MPA protection is not extended to areas that are currently most often visited, and therefore most vulnerable to impacts, by humans (CCAMLR 2011a paragraph 2iv). The LJ10S scenario is located in an area that is rarely,

if ever fished (CCAMLR 2017), is far south of the majority of research stations in the region (Council of Managers of National Antarctic Programs 2017), and experiences very few visits from tourists (Lynch et al. 2010).

In contrast, the LJ10 scenario performed better than the LJ10S scenario in terms of the objectives laid out in the General framework for the establishment of the CCAMLR Marine Protected Areas (CCAMLR 2011a paragraph 2). The LJ10 scenario nearly spans the length of Statistical Subarea 48.1 and includes both northern and southern areas. It includes habitat for species that are not protected in the LJ10S scenario such as *G. gibberifrons* (Iwami and Kock 1990, Kock and Jones 2005). As such, the LJ10 scenario contains a more representative sample of habitat (CCAMLR 2011a paragraph 2i). The LJ10 scenario offers protection for regions around the South Shetland Islands where Antarctic Fur seals breed (Goebel and Reiss 2014, Second WS-MPA Domain 1 2015) and includes areas important to larval krill in the Gerlache (Huntley and Brinton 1991). As such, the LJ10 scenario offers more protection for key life history stages (CCAMLR 2011a paragraph 2ii) of species of conservation interest than than LJ10S scenario. The LJ10 scenario also would protect areas that are currently vulnerable to impacts by humans (CCAMLR 2011a paragraph 2iv). This is best documented by the spatial overlap with 40% of the contemporary fishery (Watters et al. 2013), but the LJ10 scenario also includes areas near research stations and camps (Council of Managers of National Antarctic Programs 2017) and areas that are regularly visited by tourists (Lynch et al. 2010). It is likely that the amount of spatial overlap with the current fishery, would prove a challenge to advancing the LJ10 scenario as a proposal to the CCAMLR.

However, if this scenario's fishery impacts were to be framed in terms of the more modest impact on future catches, it might be received more favorably.

An ideal MPA scenario, one that improved biomass outcomes for all declining species and minimized spatial overlap with fisheries, was not identified. However, the LJ10 and LJ10S scenarios both improved biomass outcomes for three species, the LJ10 scenario appeared to satisfy a number of objectives laid out in CM 91-04 (CCAMLR 2011a), and Ecospace simulations indicated the two scenarios would have similar modest impacts on catch. These scenarios highlighted the importance of protecting the southern area where Ecospace indicates krill will concentrate. The LJ10S scenario significantly minimized spatial overlap with the current fishery, but fell short of meeting several of the goals laid out in CM 91-04. The LJ10S scenario might seem like a residual MPA because it is in an area that is not currently utilized by the fishery, but it does protect an area that simulations indicate may be of interest to the fishery in the future. There might be significant political motivations to elevate minimizing displacing the current and future fishery such that a residual MPA is created (Devillers et al. 2014). Such an MPA may not be effective in helping the CCAMLR achieve its conservation goals or meet the objectives described in CM 91-04. It may be possible to adjust the boundary configuration of the LJ10 scenario to reduce spatial displacement of the current fishery while still providing effective protection to the southern regions where the model indicates krill will concentrate in the future. Such a compromise MPA boundary configuration could help the CCAMLR achieve some of its conservation goals.

It is worth noting that there is uncertainty associated with simulation outcomes for where krill will aggregate in the future and for outcomes regarding MPA performance. The Ecospace simulation was tuned to the available data (Chapter 3), but was not able to recreate directional movement patterns of krill. It is widely recognized that there is much uncertainty regarding krill movements (Watters et al. 2013) and the Ecospace simulations were not able to bound that uncertainty. Additionally, the sea-ice scenarios were created using data from 1996-2012. If future sea-ice conditions significantly differ from conditions that occurred during those years, simulation outcomes may not be informative. Findings from Ecopath with Ecosim simulations are often described as “strategic not tactical” (Link et al. 2012). It may be valuable to consider that perspective when reviewing the results of the MPA simulations. The specific boundaries of the LJ10 and LJ10S scenario may matter less than the fact that they protect a southern area where krill may concentrate in the future.

Summary and Conclusions

The simulations presented in this chapter demonstrate that Ecospace is an effective tool to evaluate how potential MPA boundaries could affect patterns of biomass accumulation. Four different MPA scenarios were explored, and each had some impact, at least at the highest fishing level. The far southern region of Statistical Subarea 48.1, protected in the LJ10 and LJ10S scenario, slowed population declines for Antarctic fur seals, Adélie penguins and krill. The LJ10S scenario spatially overlaps with less than 1% of the current fishery, and Ecospace indicates that protecting this region would decrease catches by 10-14% compared to the absence of an MPA. Protecting the LJ10S scenario as

a standalone MPA may not sufficiently meet objectives laid out in the the General framework for the establishment of CCAMLR Marine Protected Areas (CCAMLR 2011a). Specifically, the LJ10S scenario may not protect a representative sample of biodiversity in the region, fails to protect key habitats at all life stages for some currently monitored species, and may not protect the areas vulnerable to anthropogenic impacts. The LJ10 scenario better meets the objectives laid out in CM 91-04, but the fact that it would displace 40% of the current fishery may pose a challenge for advancing this MPA scenario. However, simulation outcomes indicate that its impact on the fishery could actually be as low as 9-14% reduced catch if future spatial fishing patterns are considered. It may be possible and desirable to adjust the boundaries of the LJ10 scenario to the minimize overlap with the current fishery while preserving protection in the southern region.

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CHAPTER FIVE: GENERAL CONCLUSIONS

Introduction

The work presented throughout this dissertation represents the early stages of a systematic conservation planning (SCP) process (Margules and Pressey 2000, Gaston et al. 2002, Kukkala and Moilanen 2013). It was designed to complement the ongoing SCP process in the CCAMLR (Second WS-MPA Domain 1 2015). As described by Gaston et al. (2002) the early stages of SCP include defining the study area, compiling relevant biodiversity data, and identifying conservation objectives.

To that end, the study area was narrowed from the larger Planning Domain 1 (CCAMLR 2011b, Second WS-MPA Domain 1 2015) to Statistical Subarea 48.1 which lies in the center of Planning Domain 1. The study area was narrowed because ecologic and environmental data are concentrated in this region. The “General framework for the establishment of CCAMLR Marine Protected Areas” requires that MPA decisions be based upon the best available science (CCAMLR 2011a paragraph 2), and to date the CCAMLR has shied away from making MPA decisions in data sparse regions (Brooks et al. 2016). Statistical Subarea 48.1 is the one region of planning Domain 1 for which abundant data exist to plan an MPA and in which no MPA currently exists. Therefore, it seemed likely to be more useful to the CCAMLR, and more likely to result in an adequately performing ecosystem model, to focus on Statistical Subarea 48.1

Next, data were compiled describing both biodiversity values and human use patterns. The data used in the official CCAMLR process focus solely on patterns of spatial distribution and rely heavily on static maps (Second WS-MPA Domain 1 2015). The goal of the work presented throughout this dissertation was to develop a dynamic trophic model to aid in the MPA planning process and complement the static spatial models that are being used in the official CCAMLR process. To that end, a literature search was conducted to identify publicly available data that could be used to build a mass balanced food web model (Ecopath Chapter 2), to calibrate that model using time dynamic simulation (Ecosim Chapter 2), to build a tempo-spatially dynamic version of that model (Ecospace Chapter 3), and to develop scenarios representing future conditions (Chapter 3). All of this was done with the purpose of building a dynamic model that could be used to evaluate the efficacy of potential MPA boundary scenarios in a region that is dramatically impacted by climate change (Chapter 4). As a whole, the tables presented in each chapter and the appendices provide a compilation of much of the ecosystem data that are available for the region.

While previous Ecopath food web models had been developed for the region (Erfran and Pitcher 2005, Cornejo-Donoso and Antezana 2008, Hoover et al. 2012, Ballerini et al. 2014), none of the existing models were suitable to use in the MPA process. This was for two key reasons. None of the models represented all monitored species likely to be the focus of MPA discussions as single species groups. Additionally, none of the models had been successfully calibrated using field data, which made their output less trustworthy. Work currently underway in the CCAMLR (Second WS-MPA

Domain 1 2015) is setting conservation goals for species such as Adélie and chinstrap penguins. None of the previous models treated both species as single species groups (Erfran and Pitcher 2005, Cornejo-Donoso and Antezana 2008, Ballerini et al. 2014), or were successful at recreating observed trends of abundance for these groups (Erfran and Pitcher 2005, Hoover et al. 2012). The work advanced in this dissertation corrected these two issues. Species that are likely to be important in developing protection goals and in monitoring the efficacy of the MPA have been modeled as single species groups. The model has been successfully calibrated using data for those species, making simulation outcomes for those species more trustworthy than outcomes from previous models.

The last stage of data compilation was to gather the data needed to create spatio-temporal simulations in Ecospace. This relied heavily on using the spatial data from the CCAMLR process (Second WS-MPA Domain 1 2015) to define foraging area maps, and was supplemented by data on swim speeds, and monthly maps of sea-ice concentration (Cavalieri et al. 1996, updated yearly). The simulation was tuned by selecting sea-ice response curves that helped to adequately recreate general trends in biomass accumulation patterns. Additionally, environmental data were resampled to create eight 100-year scenarios that examined the impacts of fishing pressure and reduced sea-ice (Chapter 3). Krill are known to exhibit seasonal directional movement patterns, contracting into coastal waters in the winter and moving farther off shore in summer (Reiss et al. 2017). Ecospace is not currently able to capture directional movement of krill, or even advection related to predominant winds and current forcing. This weakens the credibility of the spatial outcomes for krill. However, the model was able to recreate

the large-scale trends of decreasing biomass and shifting areas of relatively higher abundance south (Atkinson et al. 2004, Ducklow et al. 2013).

Uncertainty

Modeling inherently involves uncertainty. This uncertainty, and the failure to attempt to account for it, makes it hard to derive definitive conclusions from model output. Uncertainty can enter a model at numerous levels. There is uncertainty associated with the model framework itself (structural complexity), with the parameters entered into the model (natural variability and observation error), and with input used to develop scenarios that explore and communicate management options (Link et al. 2012). Some of these sources of uncertainty and their implications have been discussed in previous chapters. However, interpretation of results may be aided by more holistically discussing uncertainty.

Complexity of the modeling framework contributes to uncertainty in model outcomes. Whole ecosystem models are intrinsically more complex than single species models, or even minimally realistic models which seek to model only a subset of species that likely have the most significant interactions with the focus species (Plaganyi 2007, Link et al. 2012). Model complexity also varies across implementation of specific modeling frameworks. Comparing only models created using Ecopath with Ecosim, model complexity increases as the modeler adds groups to the model, progresses from Ecopath to time dynamic simulations in Ecosim, then to spatially dynamic simulations in Ecospace, and then to spatial-and temporally dynamic simulations using the external data framework. Cornejo-Donoso and Antezana (2008) presented an Ecopath model with 28

model groups. Ballerini et al. (2014) presented an Ecopath model with 24 groups. Hoover et al. (2012) presented an Ecopath model and Ecosim dynamic simulations for 54 groups. Erfran and Pitcher (2005) presented an Ecopath model, Ecosim dynamic simulations, and Ecospace spatially dynamic simulations. The model presented here, with its 35 modeled groups that are progressed through Ecopath, Ecosim, Ecospace, and spatio-temporally dynamic simulations is the most complex Ecopath model for the region. This level of complexity adds significant uncertainty to the model.

It has been argued that developing complex whole ecosystem models should be avoided to reduce model uncertainty (Fulton et al. 2003). There has been a preference in the CCAMLR modeling community to use minimally realistic models, rather than whole ecosystem models, to help inform fisheries management (Hill et al. 2006, Hill et al. 2007, Plaganyi and Butterworth 2012, Watters et al. 2013). Two minimally realistic models were developed to explore krill fisheries management in the Western Antarctic Peninsula and Scotia Sea region, neither model was initially designed to explore MPA issues (Plaganyi and Butterworth 2012, Watters et al. 2013). Yet for some research questions, large complex whole ecosystem models are a good choice of model framework, and the Ecopath with Ecosim framework is one of the most capable at addressing a wide variety of policy issues. (Plaganyi 2007). Even though the complexity adds significant uncertainty, the simulations presented here, using spatially and temporally dynamic sea-ice, may be a good way to explore MPA design in a rapidly changing region.

Regardless of the model framework, uncertainty is introduced with each parameter due to natural variability and observation error (Link et al. 2012). In the

Western Antarctic Peninsula region, uncertainties related to natural krill mortality, krill movement patterns, and predator responses to krill availability are widely recognized (Watters et al. 2013). Modelers working within the CCAMLR system have collated a set of input parameters related to life history patterns and consumption rates of krill by certain predators; for these estimates they have reported measures of uncertainty associated with the data such as 95% confidence intervals, averages, and extreme values (Hill et al. 2007, Link et al. 2012). Such bounding of the uncertainty associated with the data is a best practice for how to consider uncertainty related to variability and observation error (Link et al. 2012). On-going modeling efforts within the CCAMLR continue to use these bounded parameters (for example Plaganyi and Butterworth 2012, Watters et al. 2013) and the Ecopath model developed for this dissertation also drew heavily from Hill et al. (2007). However, not all of the groups included in the Ecopath model were represented in the Hill et al. (2007) parameters, and for those groups there is an undocumented amount of uncertainty associated with their Ecopath input parameters.

Another significant source of uncertainty in the Ecopath model is the diet matrix (Link et al. 2012). This was acknowledged in the model balancing process. Diet compositions, rather than other parameters, were adjusted to bring the model into balance because of the high level of uncertainty associated with them. However, this balancing process introduced more uncertainty into the model as diets were adjusted. Parameters detailed by Hill et al. (2007) include bounded estimates of amount of krill consumed by select predators, and as such could not be entered directly into the more detailed Ecopath diet matrix.

Advancing the model to Ecosim simulations allows for the possibility of calibrating the model and performing the best practice (Hill et al. 2006) of running Monte Carlo simulations to assess model sensitivity and outcome uncertainty (Heymans et al. 2016). Monte Carlo runs identify a range of output values when input parameters are varied within a specified C.V. For the present work, the greatest variability in model outcomes, and thus highest outcome uncertainty and sensitivity, was associated with *C. gunnari* and *N. rossii*. This was not surprising as there was also high uncertainty associated with the input data for these species whose life history parameters are not well described in the literature and for which there were significant gaps in the biomass time series (Kock and Jones 2005). The Monte Carlo simulation built into EwE is a convenient means to assess input and simulation outcome variability, but modelers working in other frameworks have developed their own routines, and Monte Carlo frameworks, for assessing or bracketing model sensitivity. For example Watters et al. (2013) in their minimally realistic model of the Scotia Sea developed multiple scenarios of input parameters specifically to bracket uncertainty.

Developing the model into a spatially dynamic scenario adds flexibility to explore MPA scenarios. It also adds complexity and uncertainty related species' spatial patterns which is compounded by using imprecise spatial sea-ice response curves. Because there is currently no capacity in Ecospace to spatially calibrate the model, simulations were tuned by estimating the simulation's performance compared to broad trends documented in the literature. The tuning process was imperfect. While it successfully recreated broad

patterns, it produced some questionable results, such as chinstrap and gentoo penguins unexpectedly concentrating east of the Antarctic Peninsula.

Spatial uncertainty could have been reduced by adopting the Small Scale Management Units (SSMU) as the planning unit, rather than 100 km². Hill et al. (2007), present parameters with bounded uncertainty at the scale of SSMUs. Watters et al. (2013) also adopt this spatial scale and take full advantage of the Hill et al. (2007) parameters, for which uncertainty was described. Adopting SSMUs as planning unit size would have limited the MPA boundary scenarios to ones that align with SSMU boundaries and would not have been implementable in Ecospace which requires that all planning units are squares of uniform size. Using 100 km² planning units allowed for much more flexibility in MPA boundary evaluation, which may prove to be more informative for the MPA process. It is worth noting that scale of the planning units can significantly impact results (Alexander et al. 2016), and effects of scale were not explored in this study. Rather the scale was selected to match the scale of the CCAMLR process (Second WS-MPA Domain 1 2015) to facilitate comparisons.

Link et al. (2012) highlighted that uncertainty can enter a model through poor communication among policy makers, stakeholders and scientists. This highlights the importance of achieving clarity on the end use for the model. Knowing how model output will be ultimately be used to explore management options allows for simulations to be better designed to bracket key uncertainties.

The Ecopath model and simulations presented here were designed with aim of being informative for the CCAMLR MPA process. They were developed in close consultation with one member of the U.S. Delegation to CCAMLR (G. Watters), and with some consultation with the U.S. stakeholder community. The simulations likely could have been improved by consulting more broadly with stake holders. As an example, four fishing levels were chosen as convenient benchmarks. Wider consultation with all stake holders would have identified fishing levels that stake holders are more interested in exploring. Similarly, while it is widely acknowledged that sea-ice loss is likely to continue in the region (IPCC 2013) no spatially explicit predictions are currently available. With more clarity on management data needs, sea ice scenarios could have been more effectively designed to bracket ice conditions that stake holders are most interested in.

Several models have been developed to explore spatial planning for the krill fishery. These models include the minimally realistic model known as the spatial-multi-species operating model (SMOM; Plaganyi 2007, Plaganyi and Butterworth 2012), the minimally realistic model created in Foosa (Watters et al. 2013), the spatial model created in Marxan (Second WS-MPA Domain 1 2015), and the model and simulations progressed in this dissertation. All of these models have their unique strengths, weaknesses and assumptions that influence model output. Some of the weaknesses are shared across the models. For example fish are notably data deficient, and their life history parameters and patterns of distribution and abundance are poorly described in the literature (Kock and Jones 2005). High uncertainty regarding fish has been noted in the

parameters collated by Hill et al. (2007). The results of both the Foosa model (Watters et al. 2013) and work progressed here indicated that there is both sensitivity of the model to fish input data, and notable uncertainty related to simulation outcomes. Modelers working in each frame work attempted to bound uncertainty as much as possible.

Both the Foosa (Watters et al. 2013) and SMOM (Plaganyi and Butterworth 2012) models adopted the SSMUs as their planning unit. Because of this, they were able to rely heavily on the parameters collated by Hill et al. (2007) and thus significantly bound their input uncertainty. They also use Monte Carlo routines, and scenario bracketing to bound outcome uncertainty. The SMOM and Foosa models were not originally designed to explore MPA design, however the Foosa model is now being further developed to contribute to MPA scenario evaluation (Pers. Comm. G. Watters, NOAA-AMLR November 2017). Foosa is limited in how it can be used to explore MPA options by its SSMU based planning unit.

The worked progressed in this dissertation and the Marxan model (Second WS-MPA Domain 1 2015) use the same planning unit size of 100 km². The Marxan model currently being developed in the CCAMLR process is solely a spatial model; its algorithms do not consider trophic dynamics or food web process. Rather, the algorithms in Marxan seek to perform a spatial optimization and highlight areas that have high biodiversity and abundance, and little overlap with human activities (Ball et al. 2009). Marxan is a very effective tool for planning representative marine protected areas, but it does not have the capability of assessing impacts of the MPA on biomass accumulations

patterns. MPA scenarios derived from Marxan analyses could be run as MPA scenarios in the Ecospace model presented here.

The Ecopath model progressed through this dissertation has more unbounded uncertainty associated with it than any of the other three models for the region. However, it has greater spatial flexibility than the Foosa model (Watters et al. 2013) and it includes sea-ice dynamics and trophic interactions while the Marxan model does not (Second WS-MPA Domain 1 2015). Simulations run in Ecospace can provide information regarding MPA design that cannot be provided by Foosa or Marxan. While EwE is a powerful tool to develop ecosystem models and explore policy options, it is best used in concert with other tools for Ecosystem based management (Heymans et al. 2016)

The most robust MPA planning efforts utilize several different planning tools to explore MPA design. Output from the Marxan analyses (Second WS-MPA Domain 1 2015), output from the further developed Foosa model (George Watters, Pers. Comm. November 2017) and output from the scenarios run in this dissertation can be collectively used to inform the MPA design process. All three models have their own uncertainties and assumptions. Results that are common across all three models would be more trust worthy than those produced by a single model. Areas identified as meriting protection by all three frameworks would be strong candidates for protection. Because of the use and development of these three different model frameworks, the process for establishing an MPA in Planning Domain 1 is robust. The work progressed using Ecopath with Ecosim is poised to make a meaningful contribution.

Sea-ice influences Temporal and Spatio-Temporal outcomes

The WAP has experienced dramatic changes in sea-ice extent and duration (Ducklow et al. 2007, Stammerjohn et al. 2008, Ducklow et al. 2013) which have been correlated with changes in the patterns of distribution and abundance of krill (Atkinson et al. 2004), penguins (Lynch et al. 2012), and benthic communities (Ducklow et al. 2013). It is therefore not surprising that the model calibration process highlighted that the sea-ice regime as influential in determining temporal patterns of biomass accumulation. For the model to recreate observed trends of abundance, the sea-ice regime had to be used to directly influence the population dynamics of Antarctic krill and *G. gibberifrons* and to indirectly impact the population dynamics of other species through predator-prey interactions. The sum of square difference (SS) between model outcomes and field observations decreased 65% after the sea-ice regime was included as a forcing function. Krill are thought to be ice dependent (Everson 2000), so it is expected and consistent with real world observations that the model better recreates biomass accumulation patterns when sea-ice directly influences krill population dynamics. Yet, some of the most recent field studies seem to indicate that as ice loss progresses, krill biomass accumulation patterns are not as closely linked to sea-ice conditions as previously thought (Reiss et al. 2017). The krill biomass time series used to build the model ended in 2012 and the research program on which this conclusion is based shifted to collecting krill data in a different season (Reiss et al. 2017). Currently there is no ongoing comparable data collection that could be used to extend the krill biomass time series, but it could be interesting to see if model performance declines for post 2012 low ice years. It was quite unexpected that sea-ice would directly influence *G. gibberifrons* population dynamics.

This fish species lives in the northern, historically less icy part of Statistical Subarea 48.1 and is benthic (Barrera-Oro et al. 2000, Barrera-Oro and Marschoff 2007). There was no reason to suspect that the species was ice dependent or directly influenced by ice dynamics. Yet, using the sea-ice regime to drive the model for that species decreased the SS for *G. gibberifrons* by 95%. It is likely, in this case, that the sea-ice regime is a proxy for some other environmental variable that was not included in the model.

Field researchers have noted that sea-ice conditions impact predators' ability to access prey. Antarctic fur seals seem to be more vulnerable to leopard seal predation when there is less sea-ice (Goebel and Reiss 2014). Adélie penguins seem to be more successful at capturing krill when there is more sea-ice (Hinke et al. 2007). Forcada et al. (2006) specifically hypothesize that changes in the sea-ice regime impact trophic dynamics, and that these changes in trophic dynamics have a significant impact on population dynamics. To achieve a well-fitting (low total SS) model, sea-ice dynamics had to be used to force predator-prey interactions. The model is therefore consistent with field observations that the sea-ice regime significantly influences biomass accumulation patterns, and ultimately population viability, through trophic interactions.

Previous studies have found that winter sea-ice conditions are important in determining population dynamics for some species (Siegel and Loeb 1995, Atkinson et al. 2004, Daly 2004, Hinke et al. 2007). However, due to the lack of winter variability in the sea-ice data used to calibrate the model (Stammerjohn 2013), it was not possible to use lagged winter maxima to explore the impact of the winter sea-ice regime. The decision to use summer minima came about because there was variability in summer

minima in the dataset. Using a normalized representation of annual summer sea-ice minima resulted in simulation outcomes recreating observed trends of abundance. This finding does not contradict that winter sea-ice maxima are important, or potentially more important than summer minima. Rather, it highlights that the signal from sea-ice may be strong enough that it is noticeable even when using several different indices.

It was anticipated that the sea-ice regime would have a significant impact on biomass outcomes resulting from the 100-year simulations. Ecosim results indicated that sea-ice scenario was very important in determining outcome. Yet, the sea-ice regime did not have as strong of a signal in Ecospace simulation outcomes for relative biomass. This also held true when MPA scenarios were evaluated; fishing level and MPA had a larger impact than ice condition. The sea-ice regime may not have as strong a signal in spatial simulation outcomes for biomass accumulation patterns for several reasons, but it is still driving the underlying time dynamic model and exerting an influence. The lack of strong spatial sea-ice signal could result from the sea-ice scenarios being too similar. It is possible that the equation used to bias selection towards low ice years was too conservative, and the resulting scenarios were too similar spatially to sharply differentiate them. It is also possible that the years 1996-2012 did not contain extreme enough region wide low ice conditions to represent what could happen as ice loss progress. In the decreasing ice scenario, animals may have been able to successfully follow favorable ice conditions, even in the lowest ice years, and thus dull the impact of ice scenario. Significant sea-ice loss has been predicted for the area (IPCC 2013), and yet much uncertainty remains about the spatial dimensions of sea-ice loss. No spatially explicit

predictions for future ice conditions in the WAP are available. Thus, for now, the Ecospace results which do not illustrate dramatic differences across the ice scenarios, seem to provide the most up-to-date perspective.

Marine Protected Area Scenarios

Conservation priorities and objectives are also set in the early stage of an SCP process. This involves a wide range of activities from determining the species that are important to protect, to determining more specific conservation goals (Kukkala and Moilanen 2013). Selecting groups to be in the initial Ecopath model effectively narrowed the species that could be considered for protection. Included in the model as single species groups were all species in the region that are regularly monitored in the CCAMLR Ecosystem Monitoring Program (Agnew 1997) as well as charismatic species, such as whales, that may be of interest to the broader conservation community.

Using Ecospace to explore MPA scenarios also narrowed the types of conservation goals that could be examined. While the official CCAMLR process (Second WS-MPA Domain 1 2015) is focused on ensuring that MPA scenarios are representative and protect specified percentages of the populations of species of interest (Second WS-MPA Domain 1 2015), analyses in Ecospace explored the potential impact of MPA boundary scenarios and fishing level on biomass accumulation patterns. Such an analysis is consistent with the objectives for MPAs laid out in the “General framework for the establishment of CCAMLR Marine Protected Areas” (CCAMLR 2011a paragraph 2), specifically that protection seeks to preserve ecosystem processes and functions, and lead

to the long-term viability and integrity of protected species. Ecospace specifically addresses whether a particular boundary configuration would be likely to result in more or less biomass of a given species, and thus gives insight into whether the MPA would contribute to long-term viability of the modeled species. Scenario exploration in both Ecosim and Ecospace indicates that species that are currently in decline are unlikely to return to 1996 levels, a result that is consistent with the finding of other modeling frameworks for the region (Watters et al. 2013). This result effectively limits appropriate protection goals to slowing the decline of a species.

Three of the four MPA scenarios evaluated were developed from a GIS exercise conducted with U.S. stakeholders (Watters 2015). U.S. stakeholders identified conservation objectives of interest, and then illustrated their spatial conservation priorities on the map. The conservation objectives articulated by U.S. stakeholders were not precisely measurable or directly actionable. Rather they articulated something more akin to guiding principles such as: protect krill spawning and larval development, study climate impacts separate from fishing, preserve integrity of existing studies (Watters 2015). Simulations in Ecospace are capable of determining, to some extent, if simply protecting the areas of highest priorities to U.S. stakeholders would help achieve their goals related to protecting krill and the integrity of existing studies. Specifically, Ecospace can examine whether an MPA boundary scenario would result in higher relative biomass accumulations, and if that biomass would maintain its concentrations within areas of interest to U.S. stakeholders. Protecting only the areas that represent the areas rated as the highest 5% (Watters 2015), did not appear to meet the conservation

principles espoused by U.S. participants. Ecospace simulations indicated the LJ5 MPA scenario would have little or no impact on krill or monitored krill predators under the current level of fishing. Expanding the MPA scenario to participants' top 10% prioritized areas (LJ10) or even just the southern half of their 10 % prioritized areas (LJ10S), resulted in simulation outcomes indicating a positive impact on krill and some krill predators at the current level of fishing. Both the LJ10 and LJ10S scenario seemed to concentrate krill near the Palmer LTER study area (Ducklow et al. 2007, Ducklow et al. 2013). The LJ10 and LJ10S scenarios therefore performed better at conserving krill and maintaining the integrity of existing studies.

MPA scenario evaluation further highlighted that MPA size seems to play an important role, in determining MPA efficacy, even when all considered scenarios are well above the large MPA threshold of 10,000 km² (Ban et al. 2017). While larger MPAs are known to perform better than smaller ones (Gaines et al. 2010), this effect could be related to the spatial ecology of the ecosystems the MPAs seek to protect. MPA impact of the four evaluated scenarios stratified by size. It was unexpected that the APW scenario, which was not as advantageously sited near the area of krill aggregation had a larger positive impact than the smaller but better sited LJ5 scenario.

The LJ10 and LJ10S scenario illustrated the importance of the southern area where krill aggregate in Ecospace. Comparison of the LJ5, LJ10 and LJ10S scenarios indicated that when all considered MPAs are located in the region of krill concentration, the total size of the MPA seems to matter less than the amount of this high-quality krill habitat protected. This southern region of krill concentration seems to give more

resilience to the system, particularly as sea-ice decreases. It may be politically palatable to protect the area where Ecospace simulation outcomes indicate that krill will concentrate due to the low level of fisheries activity there (CCAMLR 2017).

Setting aside solely the southern area of krill concentration (LJ10S) may not be sufficient to meet the goals laid out in the “General framework for the establishment of CCAMLR Marine Protected Areas” (CCAMLR 2011a). This region could form an integral part of a larger MPA. The simulations did not identify any other areas that are likely to increase biomass accumulation. However, the result that the APW scenario had a greater positive impact than the seemingly better sited LJ5 scenario implies that, even if sited in less than ideal habitat, a large enough MPA could have a positive impact on biomass accumulation patterns. It may thus be advantageous to protect a large area in the northern part of Statistical Area 48.1 in addition to the southern area protected by the LJ10S scenario. The aim for this northern region could be to address goals laid out in the “General framework for the establishment of the CCAMLR Marine Protected Areas” (CCAMLR 2011a) that were not met by the LJ10S scenario. For example, attempts to identify additional areas for protection might seek to increase representativeness in the species and habitats protected and to cover areas that are more immediately vulnerable to impacts by human activities.

MPA scenario exploration also illustrated that MPA impacts take over a decade to materialize, and the full effects may not be realized for several more years. This is consistent with the wider literature that indicates that older MPAs perform better, and have greater measurable impacts (Gell and Roberts 2003, Edgar et al. 2014). The length

of time an MPA takes to realize a positive impact is important when considering a “sunset clause” and when structuring monitoring activities to document MPA efficacy. A well designed MPA would likely need to have some measurable success throughout the monitoring period, so that it is more likely remain in place at the conclusion of the “sunset clause”.

Policy Implications

The work progressed in this dissertation developed a dynamic food web modeling framework that can be used to assess the effectiveness of proposed MPA boundaries for Statistical Subarea 48.1. This framework could be used to evaluate any boundary configuration in Statistical Subarea 48.1 that would be of interest to the CCAMLR. While sea-ice conditions are important in driving the model, and influencing predator-prey interactions, MPA impact did not change much across ice conditions. This implies that this modeling framework maybe an effective tool, even in the face of uncertainty regarding the sea-ice regime.

The most effective MPA scenarios evaluated were the LJ10 and LJ10S scenarios, both of which positively impacted krill and two krill predators, while having a modest 10-14% impact on future fishery catches. The LJ10 scenario could be appropriate to advance to the CCAMLR, if fishery impacts were evaluated in terms of Ecospace estimated impacts on future catches rather than spatial overlap with the current fishery. Simulations indicate that the LJ10 scenario could be able to slow declines for Adélie Penguins and Antarctic fur seals, while meeting several other objectives as described in the “General framework for the establishment of the CCAMLR Marine Protected Areas”

(CCAMLR 2011a). The LJ10S scenario matched the positive impact of the LJ10 scenario, and almost entirely lacked spatial overlap with the fishery, but it fell short of meeting objectives as described in the “General framework for the establishment of the CCAMLR Marine Protected Areas” (CCAMLR 2011a).

Currently, more attention of U.S. stakeholders is focused on the coastal waters of the Gerlache Strait and Livingston Island and areas that scientists frequently visit (Watters 2015). While these areas are important because of the biodiversity in the region and the on-going scientific efforts, Ecospace analyses indicated that the more southern regions of Statistical Subarea 48.1 may have increasing importance in the coming years. Adding this southern area to MPA scenarios may give the region some resiliency in the face of climate change. Such an addition would have relatively little impact on the past or current fishery and thus may be politically easy to adopt.

The suite of MPA scenarios evaluated illustrated some strategies for developing a more effective MPA proposal. To be effective, an MPA in the WAP must be large, much larger than the 10,000 km² that is typically the minimum threshold for a large MPA (Ban et al. 2017). MPA impacts may not be noticeable within the first decade, with the greatest impacts not realized until the MPA has been in place for about 25 years. It may be helpful to consider this lag time when discussing monitor and management plans, and setting the duration of protection for the “sunset clause”.

Future Research

The Ecospace framework is a powerful tool that can be used effectively to inform MPA design discussions in the WAP. The model and simulations are performing adequately, and they are ready to be used to evaluate boundaries developed in the CCAMLR process. Model simulation outcomes would have more credibility if the model were able to capture the known directional movement patterns of krill and if more realistic predictions for future sea-ice scenarios could be used. Several lines of investigation are currently on-going for the WAP MPA design process. Using different modeling frameworks to identify areas for conservation will likely result in a robust process and an MPA that might feasibly achieve the objectives of the CCAMLR.

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APPENDICES

Appendix 1 Definition of Functional Groups

Definitions of Functional Groups

Group #	Name	Definition
1	Killer whales	<i>Orcinus orca</i>
2	Leopard Seal	<i>Hydrurga leptonyx</i>
3	Weddell Seal	<i>Leptonychotes wedellii</i>
4	Crabeater Seal	<i>Lobodon carcinophagus</i>
5	Antarctic fur seals	<i>Arctocephalus gazella</i>
6	S Elephant Seals	<i>Mirounga leonina</i>
7	Sperm Whales	<i>Physeter macrocephalus</i>
8	Blue Whales	<i>Balaenoptera musculus</i>
9	Fin Whales	<i>Balaenoptera physalus</i>
10	Minke Whales	<i>Balaenoptera bonaerensis</i> and <i>B. acutorostrata</i>
11	Humpback whales	<i>Megaptera novaeangliae</i>
12	Emperor Penguins	<i>Aptenodytes forsteri</i>
13	Gentoo Penguins	<i>Pygoscelis papua</i>
14	Chinstrap Penguins	<i>Pygoscelis antarcticus</i>
15	Adélie Penguins	<i>Pygoscelis adeliae</i>
16	Macaroni Penguins	<i>Eudyptes chrysolophus</i>
17	Flying Birds	A number of species including Southern Giant Petrel (<i>Macronectes giganteus</i>), Antarctic Petrel (<i>Thalassoica antarctica</i>), South Polar Skua (<i>Stercorarius maccormicki</i>), Wilson's Storm Petrel (<i>Oceanites oceanicus</i>), Blue Petrel (<i>Halobaena caerulea</i>), Cape Petrel (<i>Daption capense</i>), Black Browed Albatross (<i>Thalassarche melanophris</i>), White Chinned Petrel (<i>Procellaria aequinoctialis</i>), Snow Petrel (<i>Pagodroma nivea</i>), Antarctic Fulmar (<i>Fulmarus glacialisoides</i>), Balck Bellied Storm Petrel (<i>Fregatta tropica</i>).
18	Cephalopods	Squids (for example <i>Moreoteuthis sp.</i>)
19	Myctophids (Off shelf)	Members of the the Myctophidae family, including <i>Electrona antarctica</i>
20	On-shelf fish	Fish species that live on the continental shelf, excluding the three species named below
21	N. rossii	<i>Notothenia rossii</i>
22	C gunnari	<i>Champocephalus gunnari</i>
23	G gibberifrons	<i>Gobionotothen gibberifrons</i>
24	Salps	<i>Salpa thompsoni</i>
25	Benthic Invertebrates	Including Echinoderms, polychaetes and gastropods

26	Large Krill	<i>Euphausia superba</i> older than 2 years and larger than 25 mm
27	Small Krill	<i>Euphausia superba</i> younger than 2 years and smaller than 25 mm
28	Other Euphausiids	<i>Thysanoessa macrura</i> and <i>Euphausia crystallophias</i>
29	Microzooplankton	Including Dinoflagellates, aloricates, oligotrichs, other ciliates, and sarcodines *
30	Mesozooplankton	Including Calanid Copepods, Mertridia sp, and other similiar sized organisims, *
31	Macrozooplankton	Including Ostracods, Parachaueta sp, hyperiid amphipods, gamirid amphidsa following *
32	Small phytoplankton	Including Cryptophytes and nanoflagellates smaller than 20 micrometers *
33	Large Phytoplankton	Including Diatoms larger than 20 micrometers, following *
34	Ice Algae	Algae that grow on sea-ice
35	Detritus	Detritus

Appendix 2 Biomass Sources

Literature sources for biomass data used in the model

Functional Group	Biomass Source	Effective year of Estimate
Killer whales	Branch and Butterworth (2001a)	1993-1998
Leopard Seal	Forcada et al. (2012)	1999
Weddell Seal	Forcada et al. (2012)	1999
Crabeater Seal	Forcada et al. (2012)	1999
Antarctic fur seals	Hucke-Gaete et al. (2004)	2002
Southern Elephant Seals	Carlini et al. (1997)	1996
Sperm Whales	Branch and Butterworth (2001a)	1998
Blue Whales	Branch and Butterworth (2001a)	1998
Fin Whales	Hedley et al. (2001)	2000
Minke Whales	Branch and Butterworth (2001b)	2000
Humpback whales	Hedley et al. (2001)	2000
Emperor Penguins	Coria and Montalti (2000), Trathan et al. (2011)	1998
Gentoo Penguins	Hill et al. (2007)	2002
Chinstrap Penguins	Hill et al. (2007)	2002
Adélie Penguins	Hill et al. (2007)	2002
Macaroni Penguins	Woehler (1993)	1992
Flying Birds	Ribic et al. (2011)	1995-2002
Cephalopods	Jackson et al. (2002), Hoover et al. (2012)	1996
Myctophids (Off shelf)	Pusch et al. (2004), Hill et al. (2007)	1996
On-shelf fish	Kock and Jones (2005)	1998
N. rossii	Kock and Jones (2005)	1999
C. gunnari	Kock and Jones (2005)	1998
G. gibberifrons	Kock and Jones (2005)	1998
Salps	Hoover et al. (2012), Loeb and Santora (2012), Ballerini et al. (2014)	2000
Benthic Invertebrates	Ballerini et al. (2014)	2001

Large Krill	AMLR data available at: https://swfsc.noaa.gov/AERD-Data/	1996-2001
Small Krill	EwE calculated from adult biomass	1996-2001
Other Euphausiids	Estimated following Ballerini et al. (2014)	2001
Microzooplankton	Estimated following Ballerini et al. (2014)	2001
Mesozooplankton	Estimated following Ballerini et al. (2014)	2001
Macrozooplankton	Estimated following Ballerini et al. (2014)	2001
Detritus	Estimated following Hoover et al. (2012)	1996

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Appendix 3 Production to Biomass Ratio References

Literature sources for for production to biomass ratio data

Functional Group	P/B Source
Killer whales	Brault and Caswell (1993), Kuningas et al. (2014)
Leopard Seal	Jessopp et al. (2004)
Weddell Seal	Hadley et al. (2007)
Crabeater Seal	Croxall (1987)
Antarctic fur seals	Schwarz et al. (2013)
S Elephant Seals	McMahon et al. (2003)
Sperm Whales	Ralls et al. (1980)
Blue Whales	Branch et al. (2004)
Fin Whales	Hill et al. (2007)
Minke Whales	Zhang et al. (2010)
Humpback whales	Buckland (1990), Barlow and Clapham (1997)
Emperor Penguins	Jenouvrier et al. (2005a)
Gentoo Penguins	Hill et al. (2007)
Chinstrap Penguins	Hill et al. (2007)
Adélie Penguins	Hinke et al. (2014)
Macaroni Penguins	Horswill et al. (2014)
Flying Birds	Weimerskirch et al. (1987), Ainley et al. (1990), Jenouvrier et al. (2005a), Jenouvrier et al. (2005b), Dobson and Jouventin (2010)
Cephalopods	Cornejo-Donoso and Antezana (2008), (Ballerini et al. 2014)
Myctophids (Off shelf)	Hill et al. (2007)
On-shelf fish	Hill et al. (2007)
N. rossii	Kock and Jones (2005)
C. gunnari	Iverson (1998)
G. gibberifrons	Hill et al. (2007)
Salps	Ballerini et al. (2014)
Benthic Invertebrates	Cornejo-Donoso and Antezana (2008)
Large Krill	Rosenberg et al. (1986), Candy and Kawaguchi (2006)

Small Krill	Rosenberg et al. (1986), Candy and Kawaguchi (2006)
Other Euphausiids	Ballerini et al. (2014)
Microzooplankton	Ballerini et al. (2014)
Mesozooplankton	Ballerini et al. (2014)
Macrozooplankton	Ballerini et al. (2014)
Small phytoplankton	Ballerini et al. (2014)
Large Phytoplankton	Ballerini et al. (2014)
Ice Algae	Ballerini et al. (2014)

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Appendix 4 Diet Matrix References

Literature Sources for Diet Data

Functional Group	Diet References
Killer whales	Pitman and Ensor (2003), Pitman and Durban (2010)
Leopard Seal	Casaux et al. (2009), Forcada et al. (2009)
Weddell Seal	Casaux et al. (2006)
Crabeater Seal	Hückstädt et al. (2012a)
Antarctic fur seals	Casaux et al. (2003), Polito and Goebel (2010)
S Elephant Seals	Hückstädt et al. (2012b)
Sperm Whales	Pauly et al. (1998)
Blue Whales	Kawamura (1978), Pauly et al. (1998)
Fin Whales	Armstrong and Siegfried (1991), Pauly et al. (1998), Santora et al. (2014)
Minke Whales	Kawamura (1978), Armstrong and Siegfried (1991), Pauly et al. (1998)
Humpback whales	Kawamura (1978), Pauly et al. (1998)
Emperor Penguins	Klages (1989), Cherel and Kooyman (1998)
Gentoo Penguins	Miller et al. (2010), Polito et al. (2011)
Chinstrap Penguins	Lynnes et al. (2004), Polito et al. (2011)
Adélie Penguins	Lynnes et al. (2004)
Macaroni Penguins	Deagle et al. (2007)
Flying Birds	Ainley et al. (1984), Ainley et al. (1994), Malzof and Quintana (2008)

Cephalopods	Kozlov (1995), Rodhouse and Nigmatullin (1996), Phillips et al. (2001)
Myctophids (Off shelf)	Pakhomov et al. (1996), Pusch et al. (2004)
On-shelf fish	Barrera-Oro (2002), La Mesa et al. (2004)
<i>N. rossii</i>	Casaux and Barrera-Oro (2013), Jones et al. (2003)
<i>C. gunnari</i>	Flores et al. (2004), Main et al. (2009), Jones et al. (2003)
<i>G. gibberifrons</i>	Barrera-Oro (2002), Casaux and Barrera-Oro (2013), Flores et al. (2004), Jones et al. (2003) Jones et al. (2006)
Salps	Perissinotto and A. Pakhomov (1998), Pakhomov et al. (2006)
Benthic Invertebrates	Jarre-Teichmann et al. (1997), Ballerini et al. (2014)
Large Krill	Atkinson and Snýder (1997), Perissinotto et al. (1997), Atkinson et al. (2002), Ballerini et al. (2014)
Small Krill	Ross et al. (2000), Meyer et al. (2002), Meyer et al. (2003), Töbe et al. (2010)
Other Euphausiids	Hopkins (1985), Donnelly et al. (2006), Marrari et al. (2011), Ballerini et al. (2014, J. Walsh (August 2016), Unpublished Stable Isotope Data, Winter AMLR Cruise August 2016)
Microzooplankton	Froneman and Perissinotto (1996), Froneman et al. (1996), Ballerini et al. (2014)
Mesozooplankton	Hopkins (1985), Swadling et al. (1997), Pasternak and Schnack-Schiel (2001), Ballerini et al. (2014)
Macrozooplankton	Øresland and Ward (1993), Pakhomov and Perissinotto (1996), Pakhomov and Froneman (2004), Ballerini et al. (2014)

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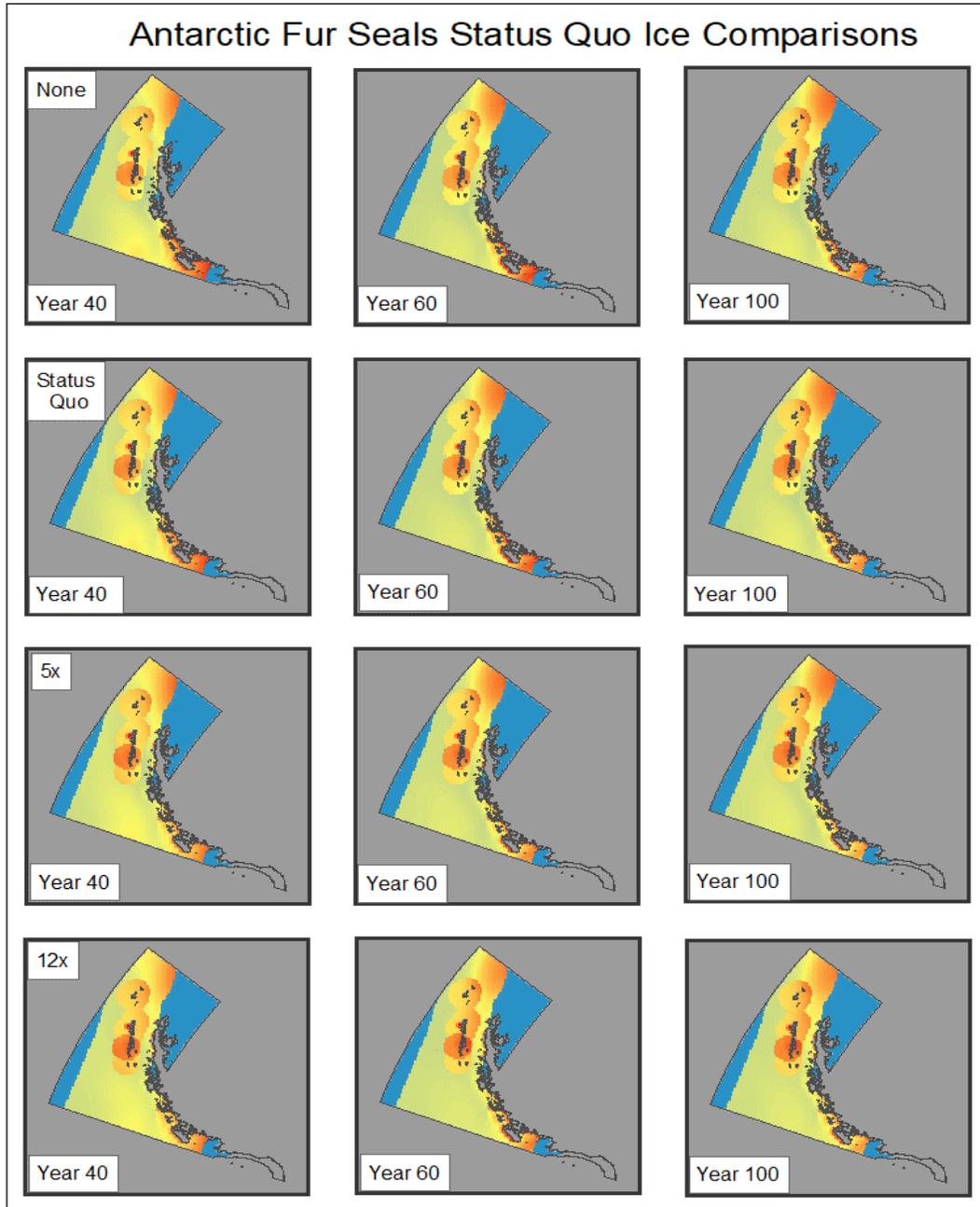
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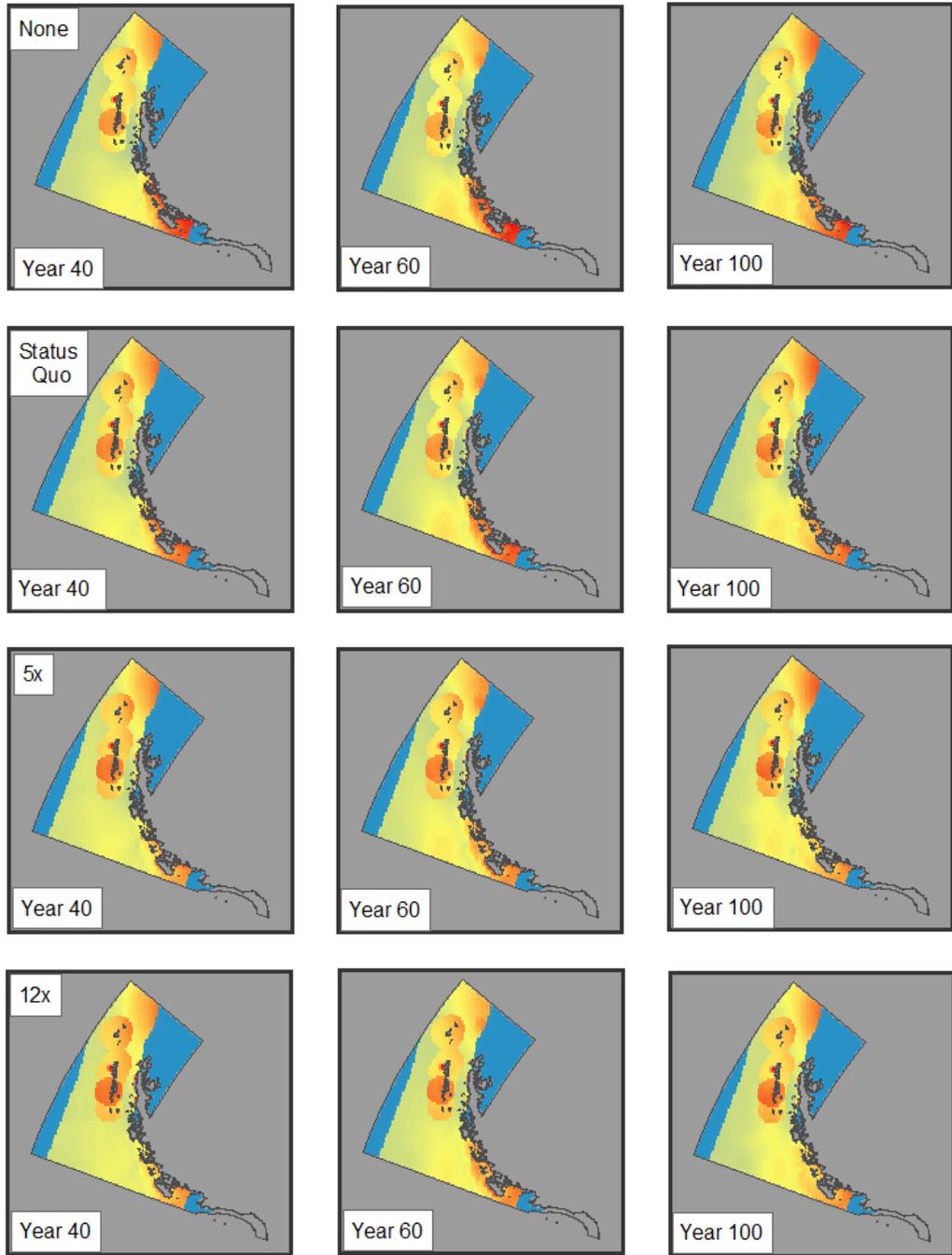
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Appendix 5 Spatial Outcomes for the Eight Monitored Species



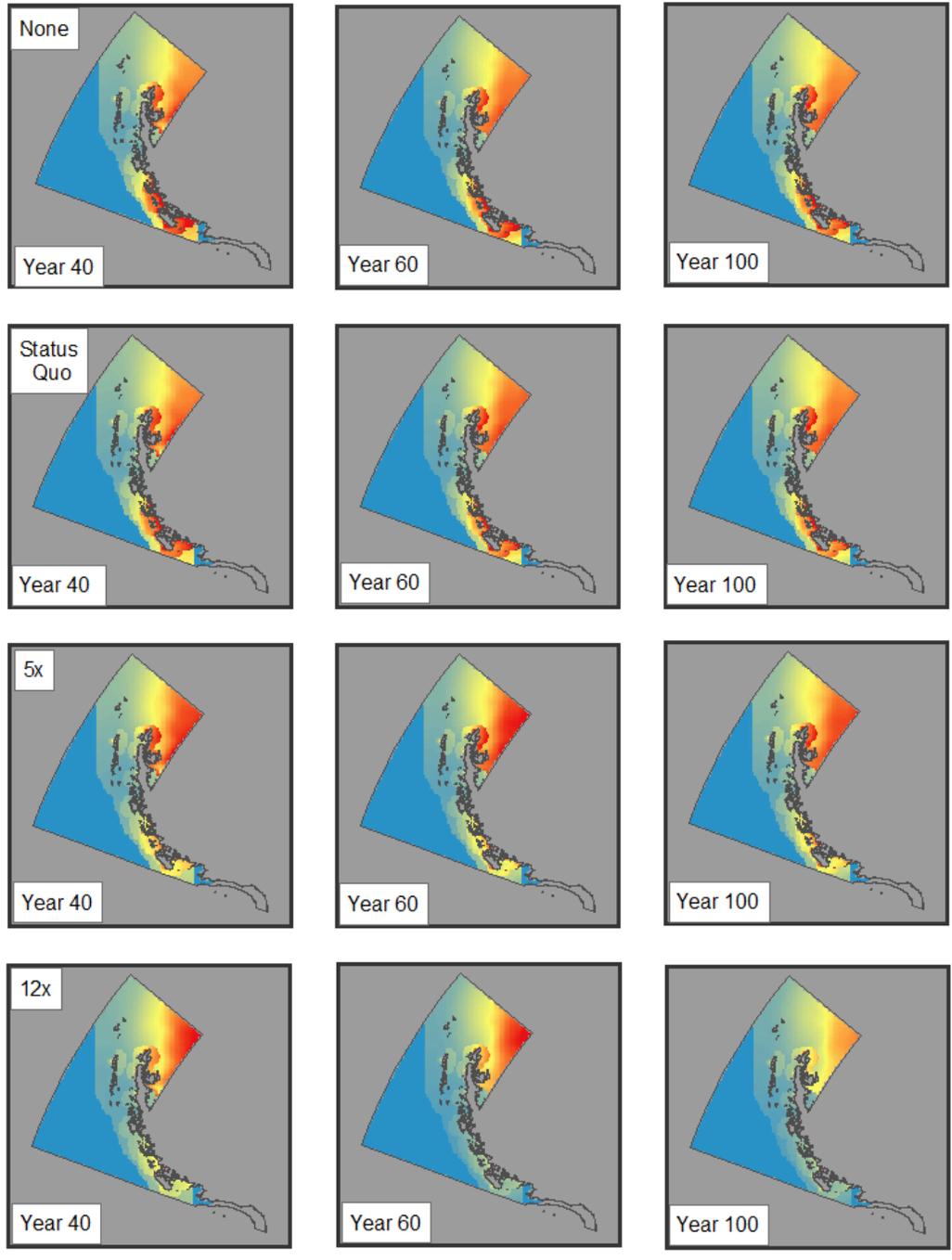
Appendix 5 i Spatial Outcomes for Antarctic fur seals in Status Quo Ice conditions. Red color indicates areas of higher concentration.

Antarctic Fur Seals Decreasing Ice Comparisons



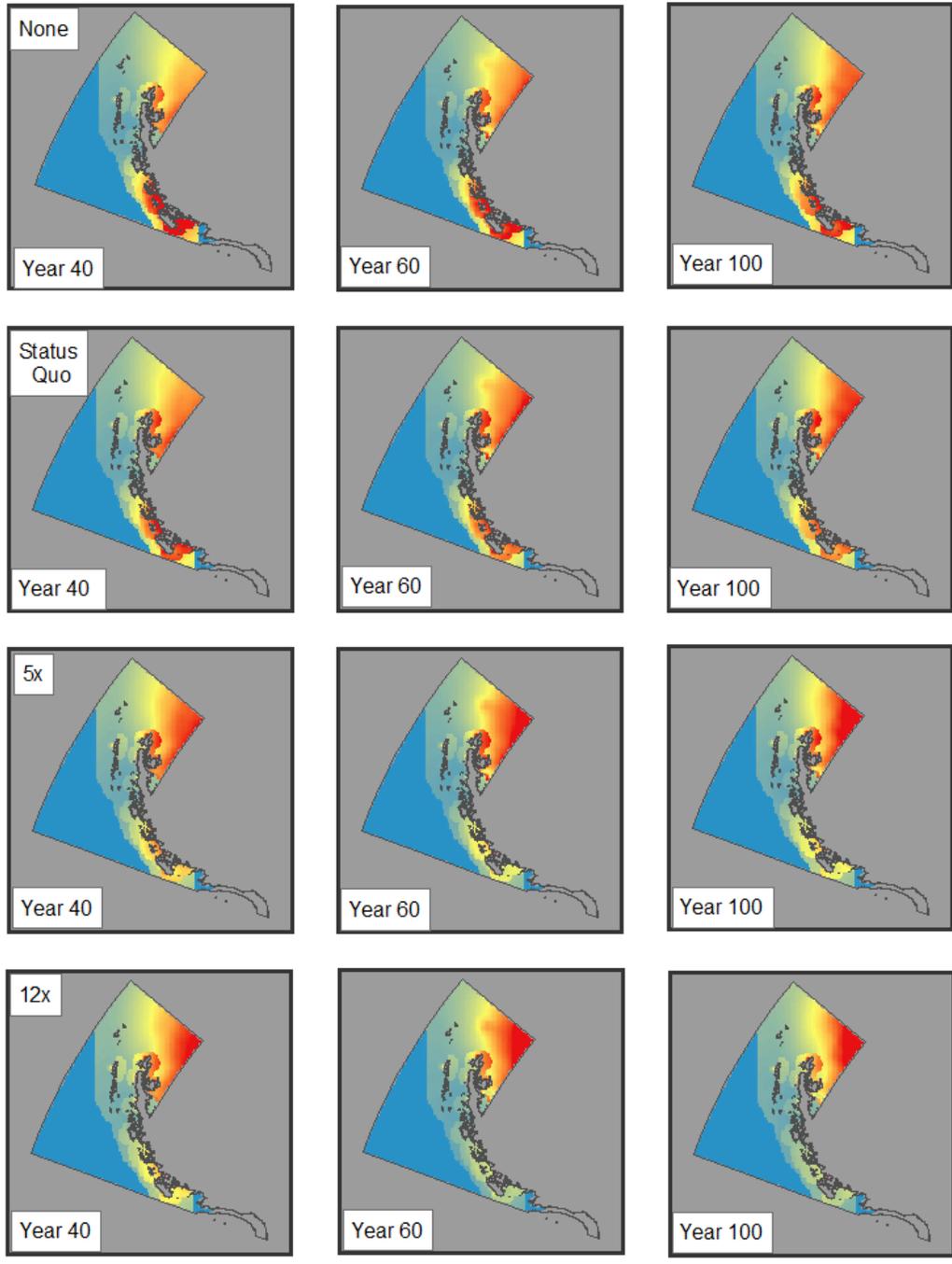
Appendix 5 ii Spatial Outcomes for Antarctic fur seals in Decreasing Ice conditions. Red color indicates areas of higher concentration.

Adelie Penguin Status Quo Ice Comparisons



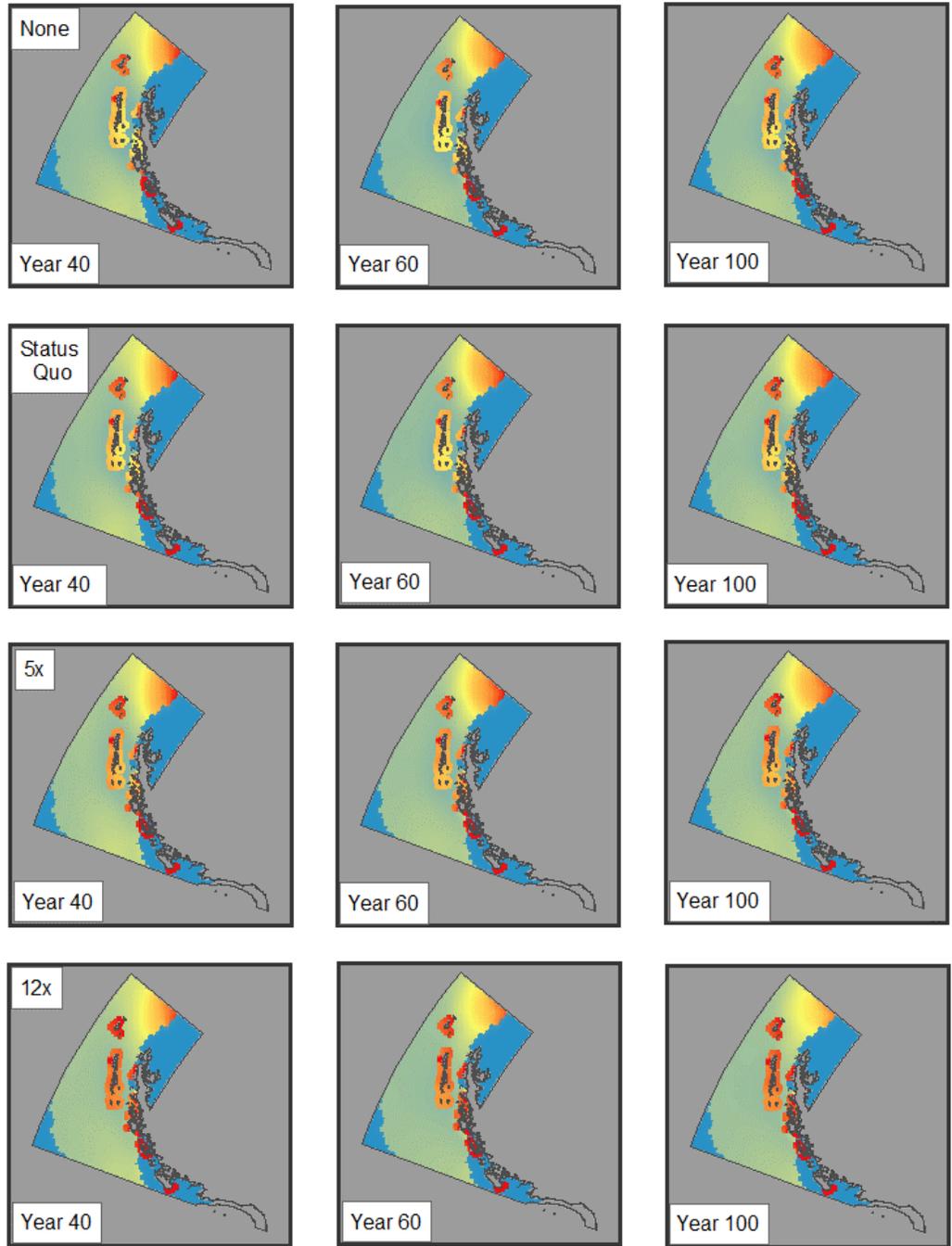
Appendix 5 iii Spatial Outcomes for Adélie Penguins in Status Quo Ice conditions. Red color indicates areas of higher concentration.

Adelie Penguin Decreasing Ice Comparisons



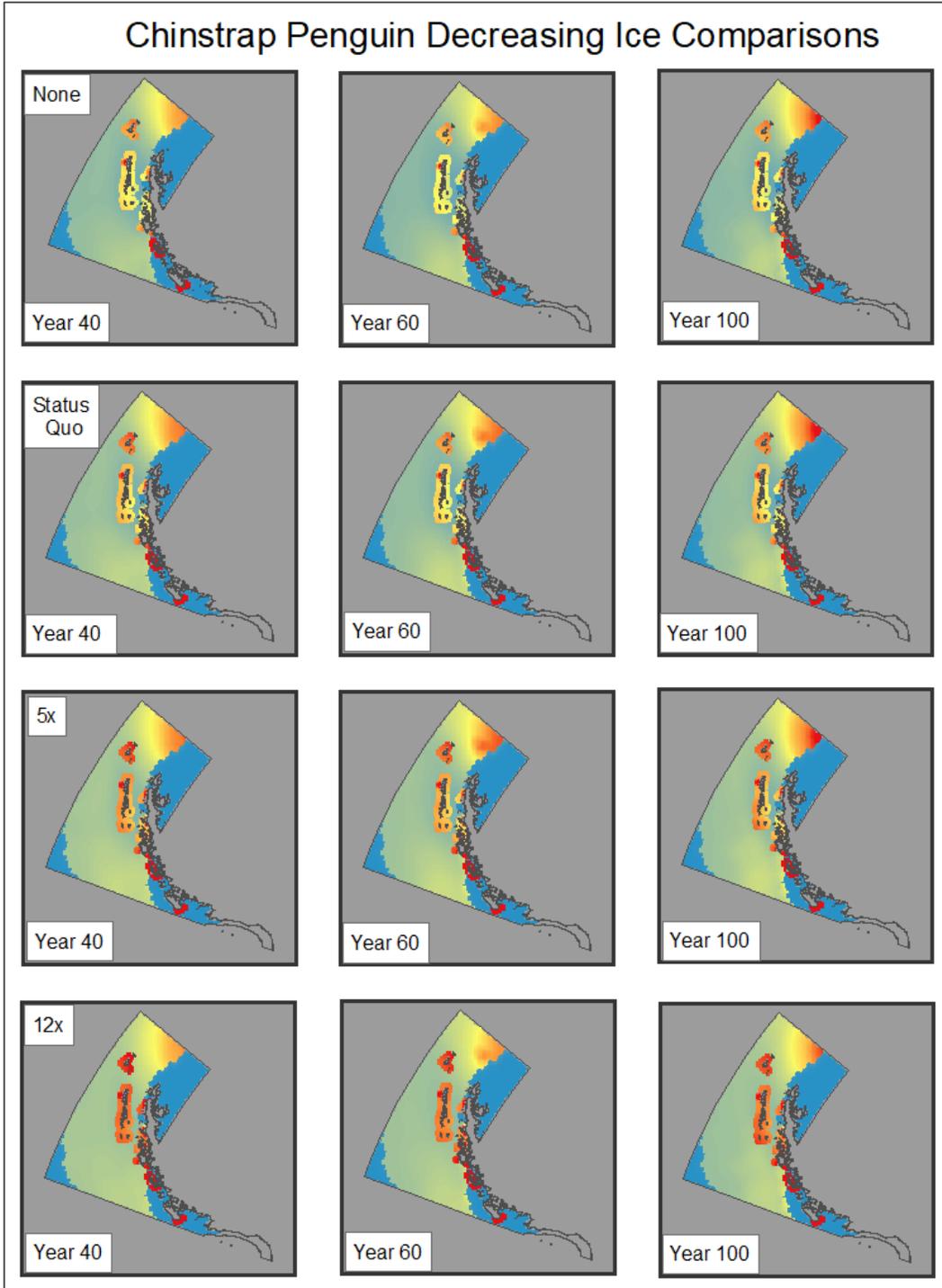
Appendix 5 iv Spatial Outcomes for Adélie Penguins in Decreasing Ice conditions. Red color indicates areas of higher concentration.

Chinstrap Penguin Status Quo Ice Comparisons



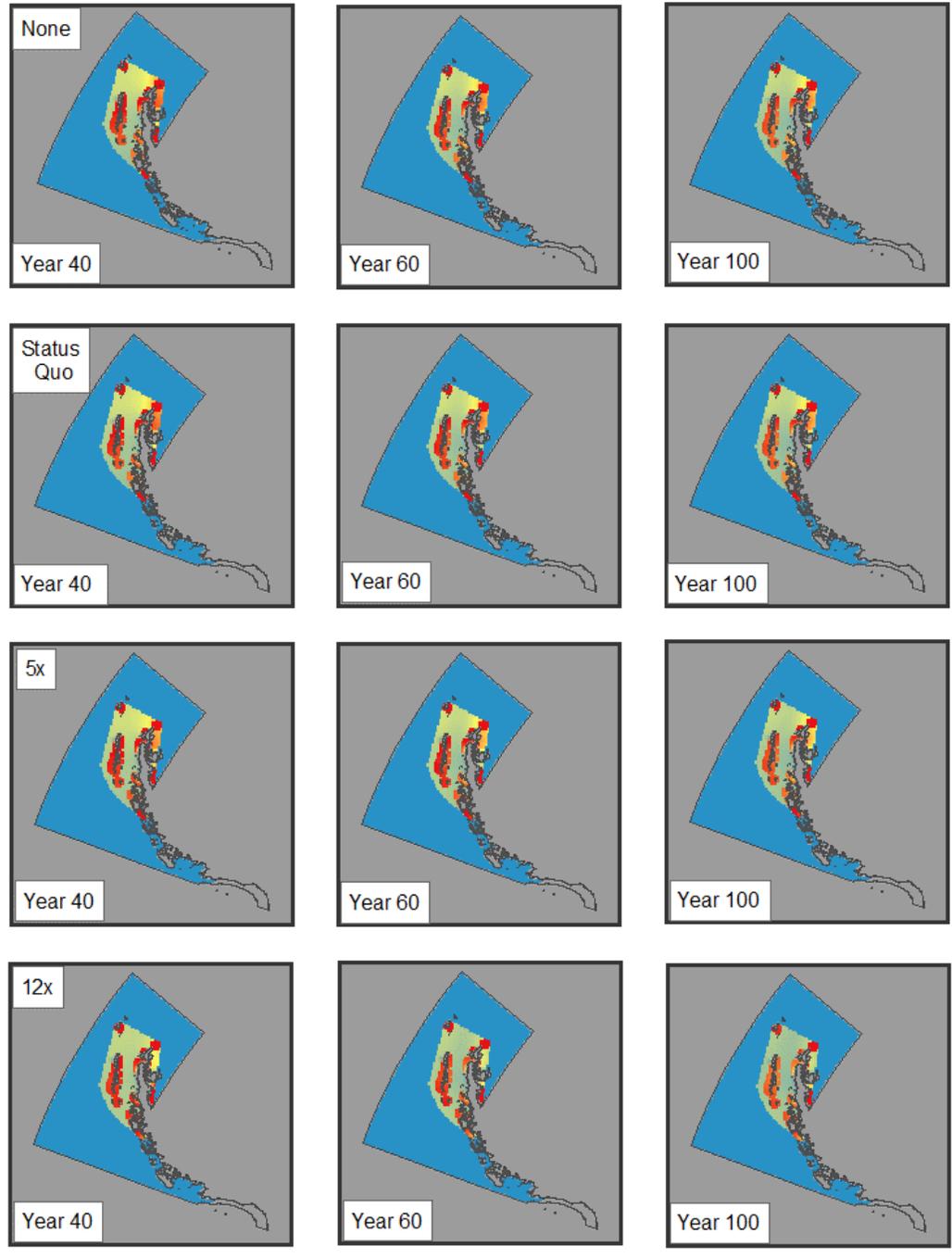
Appendix 5 v Spatial Outcomes for Chinstrap Penguins in Status Quo Ice conditions. Red color indicates areas of higher concentration.

Chinstrap Penguin Decreasing Ice Comparisons



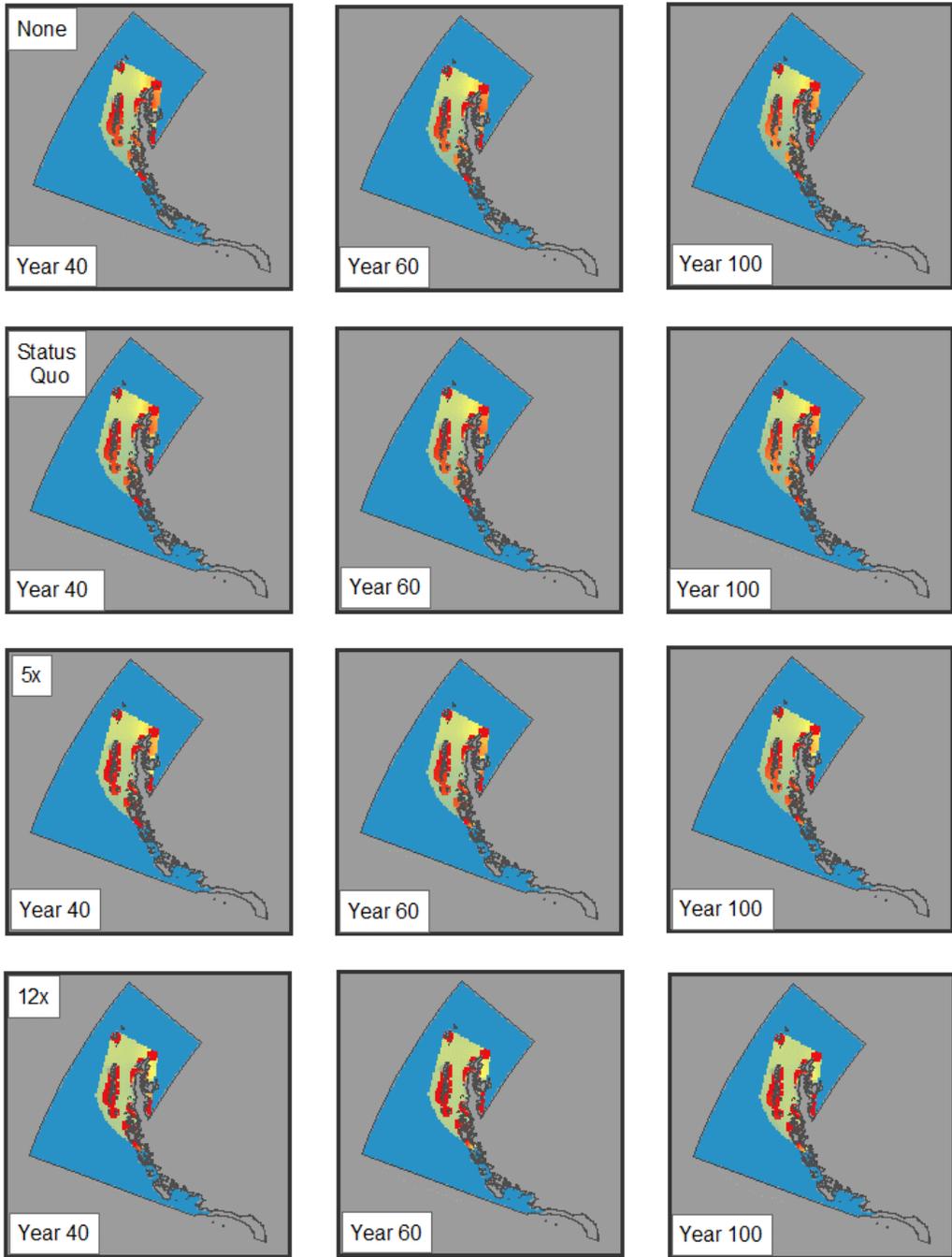
Appendix 5 vi Spatial Outcomes for Chinstrap Penguins in Decreasing Ice conditions. Red color indicates areas of higher concentration.

Gentoo Penguin Status Quo Ice Comparisons



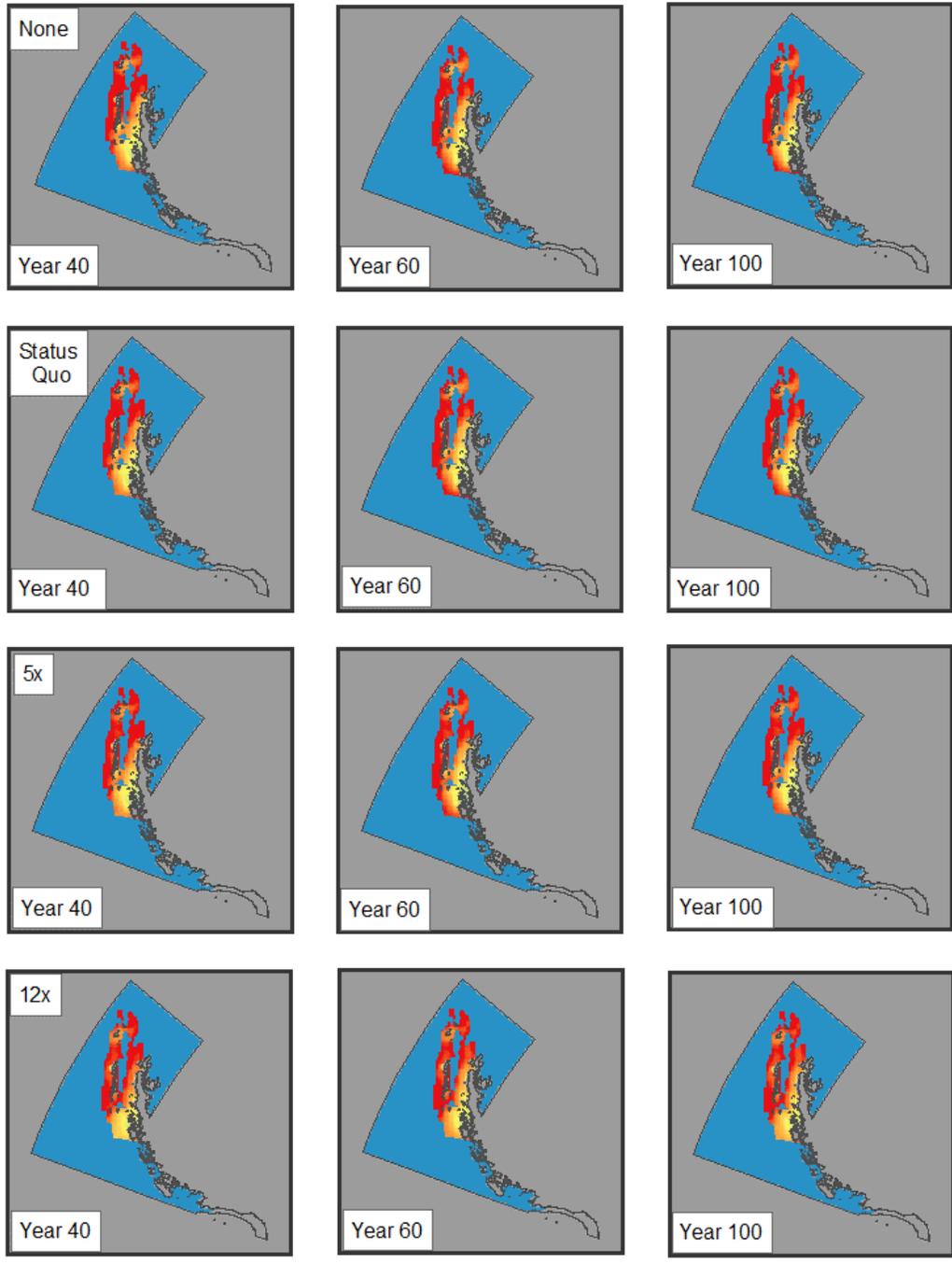
Appendix 5 vii Spatial Outcomes for Gentoo Penguins in Status Quo Ice conditions. Red color indicates areas of higher concentration.

Gentoo Penguin Decreasing Ice Comparisons

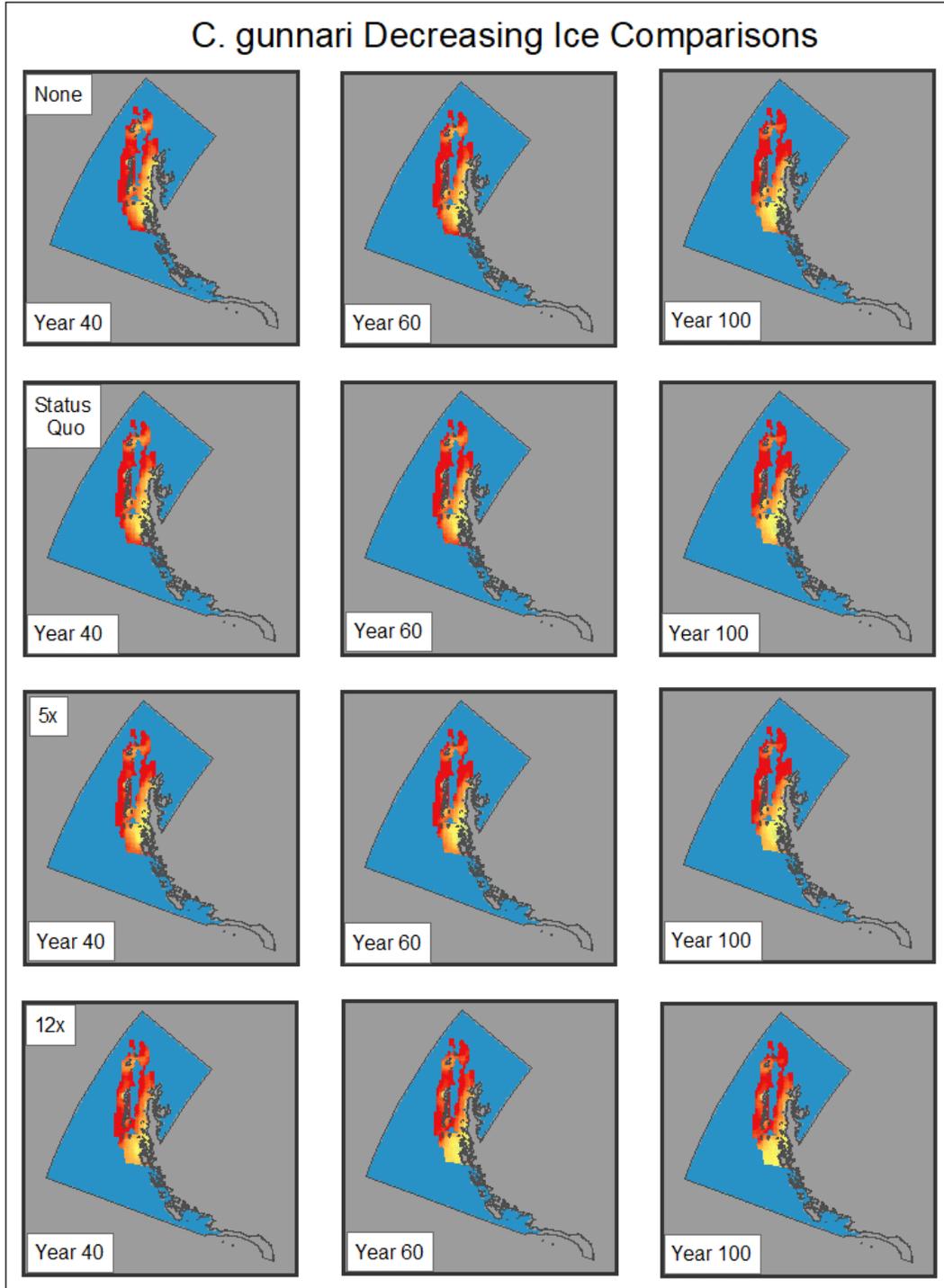


Appendix 5 viii Spatial Outcomes for Gentoo Penguins in Decreasing Ice conditions. Red color indicates areas of higher concentration.

C. gunnari Status Quo Ice Comparisons

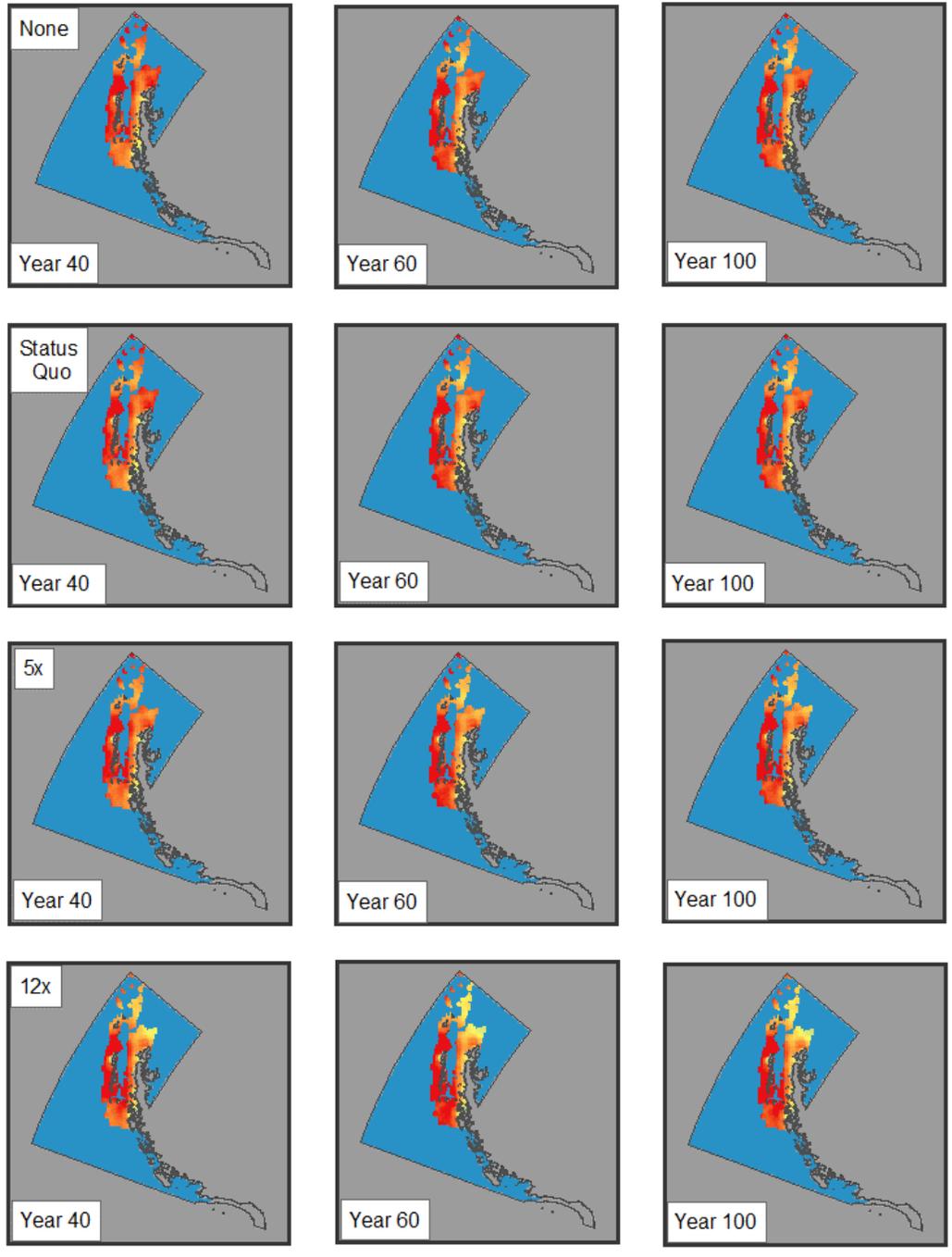


Appendix 5 ix Spatial Outcomes for *C. gunnari* in Status Quo Ice conditions. Red color indicates areas of higher concentration.

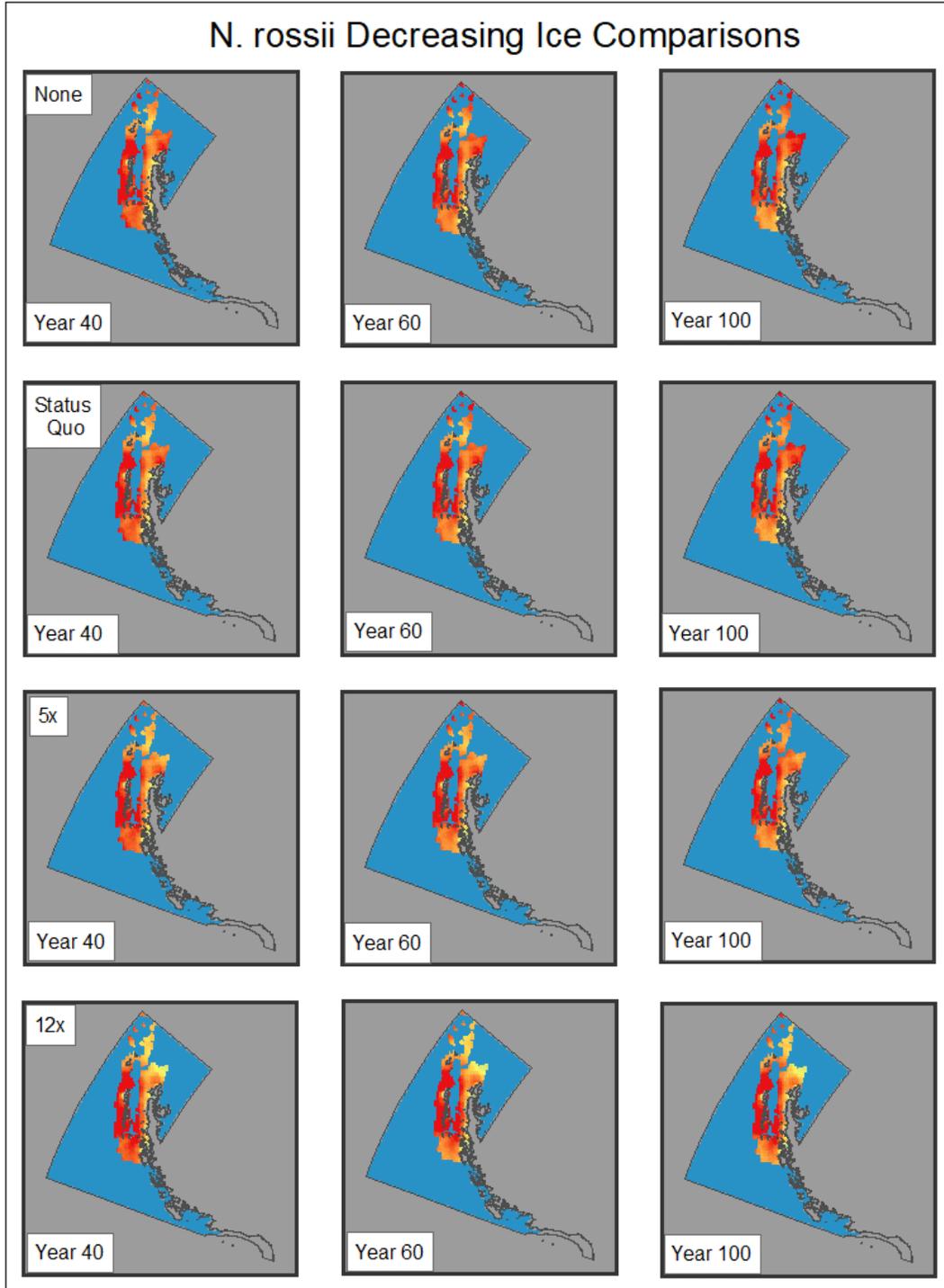


Appendix 5 x Spatial Outcomes for *C. gunnari* in Decreasing Ice conditions. Red color indicates areas of higher concentration.

N. rossii Status Quo Ice Comparisons

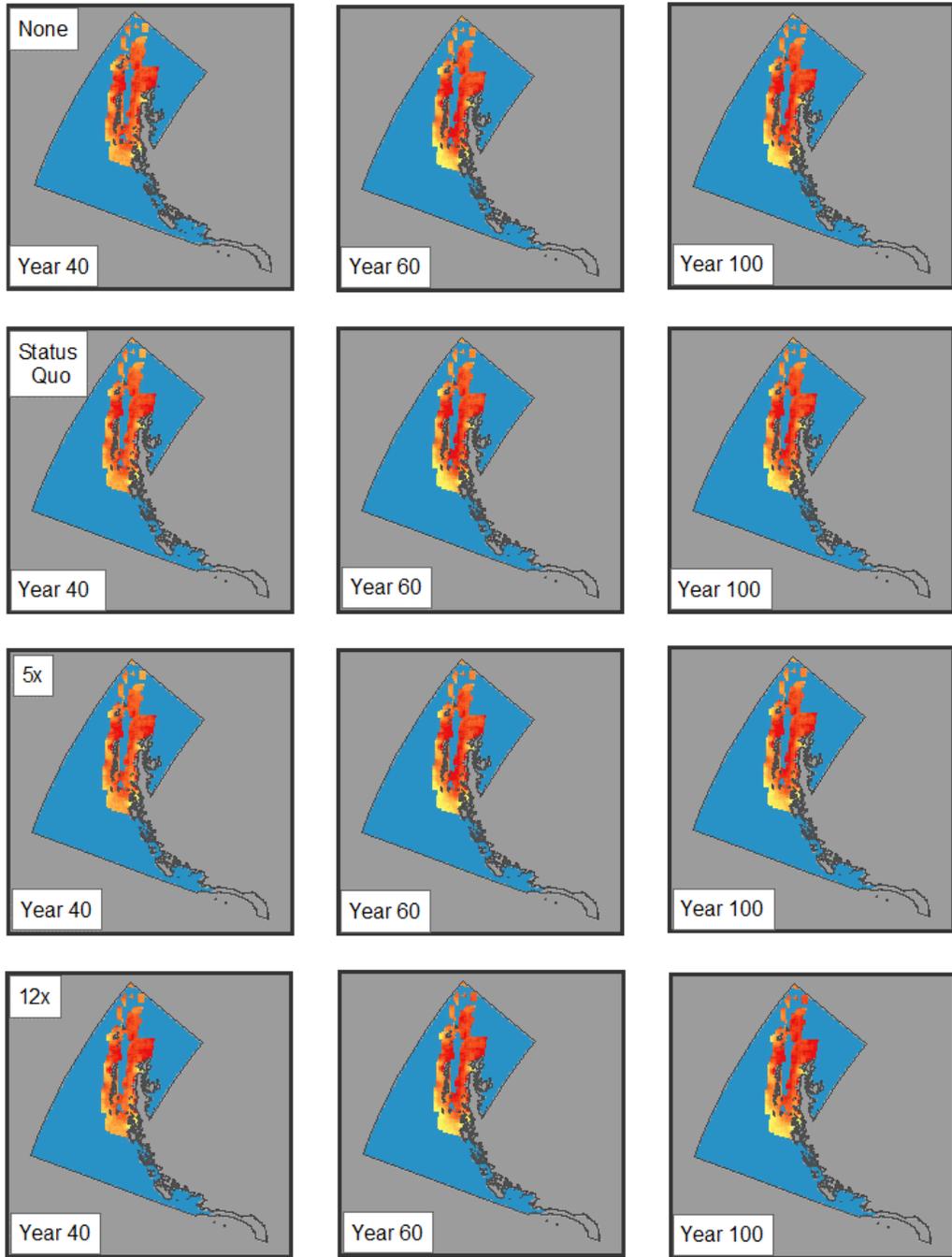


Appendix 5 xi Spatial Outcomes for *N. rossii* in Status Quo Ice conditions. Red color indicates areas of higher concentration.



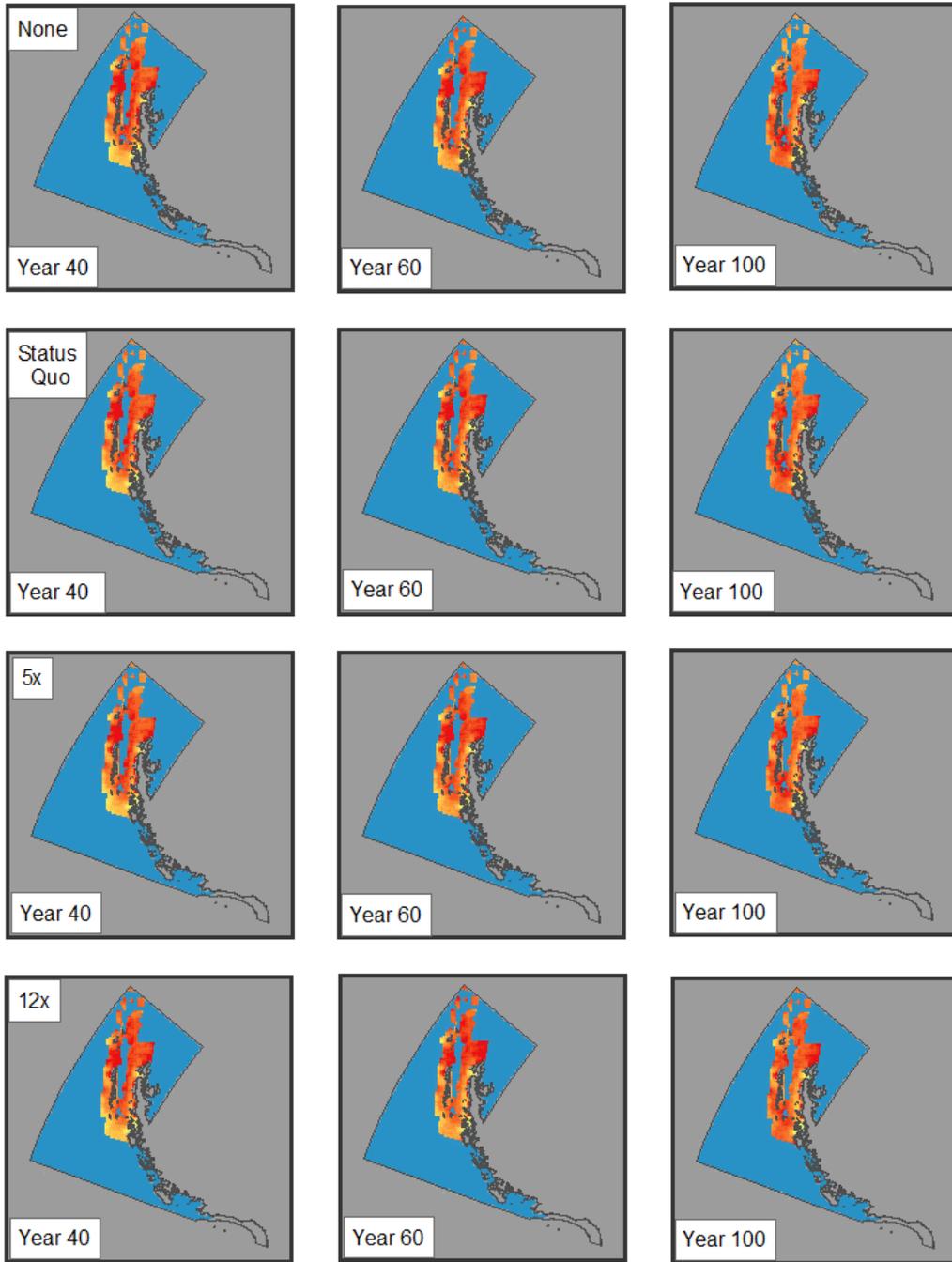
Appendix 5 xii Spatial Outcomes for *N. rossii* in Decreasing Ice conditions. Red color indicates areas of higher concentration.

G. gibberifrons Status Quo Ice Comparisons



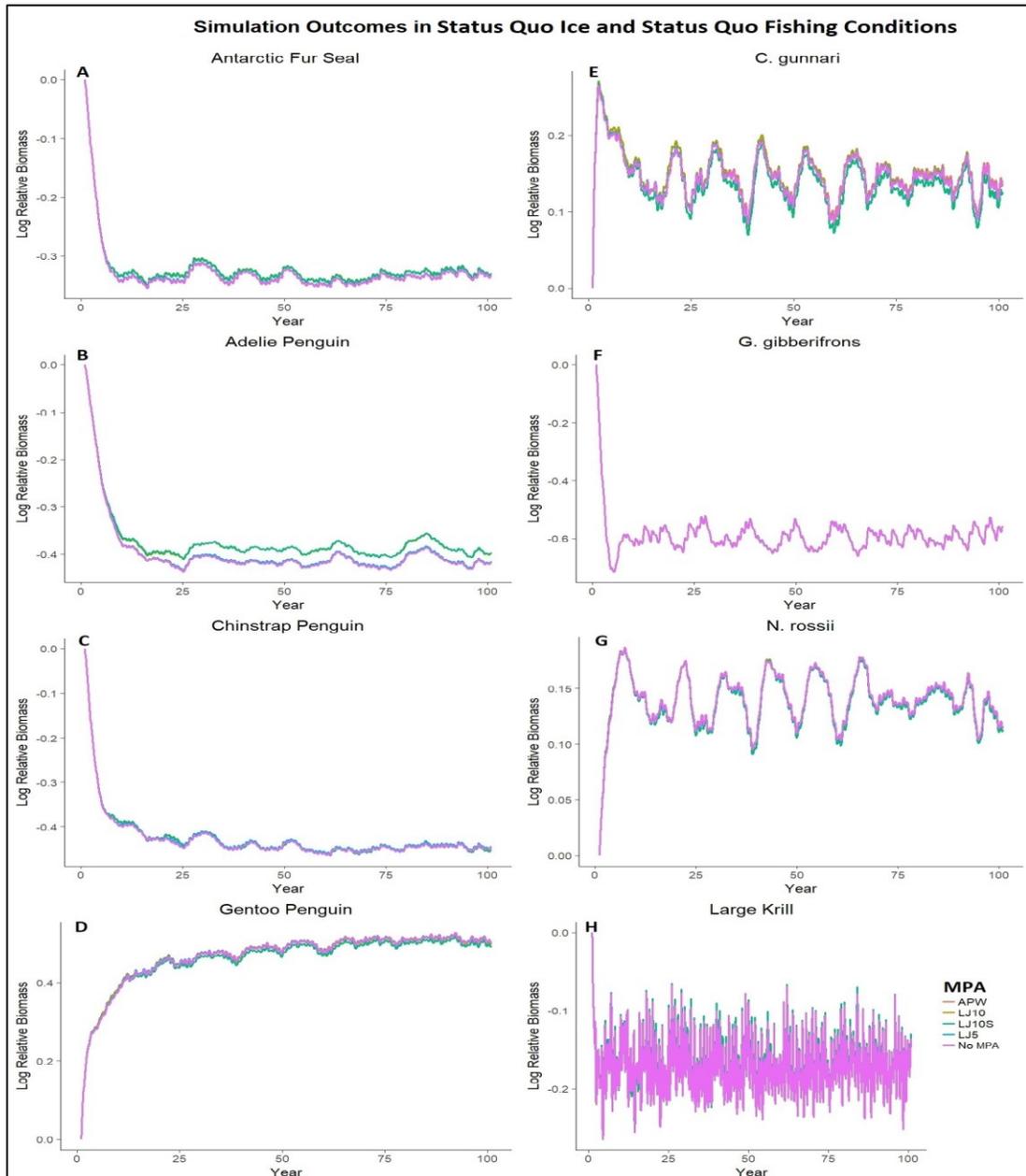
Appendix 5 xiii Spatial Outcomes for *G. gibberifrons* in Status Quo Ice conditions. Red color indicates areas of higher concentration.

G. gibberifrons Decreasing Ice Comparisons

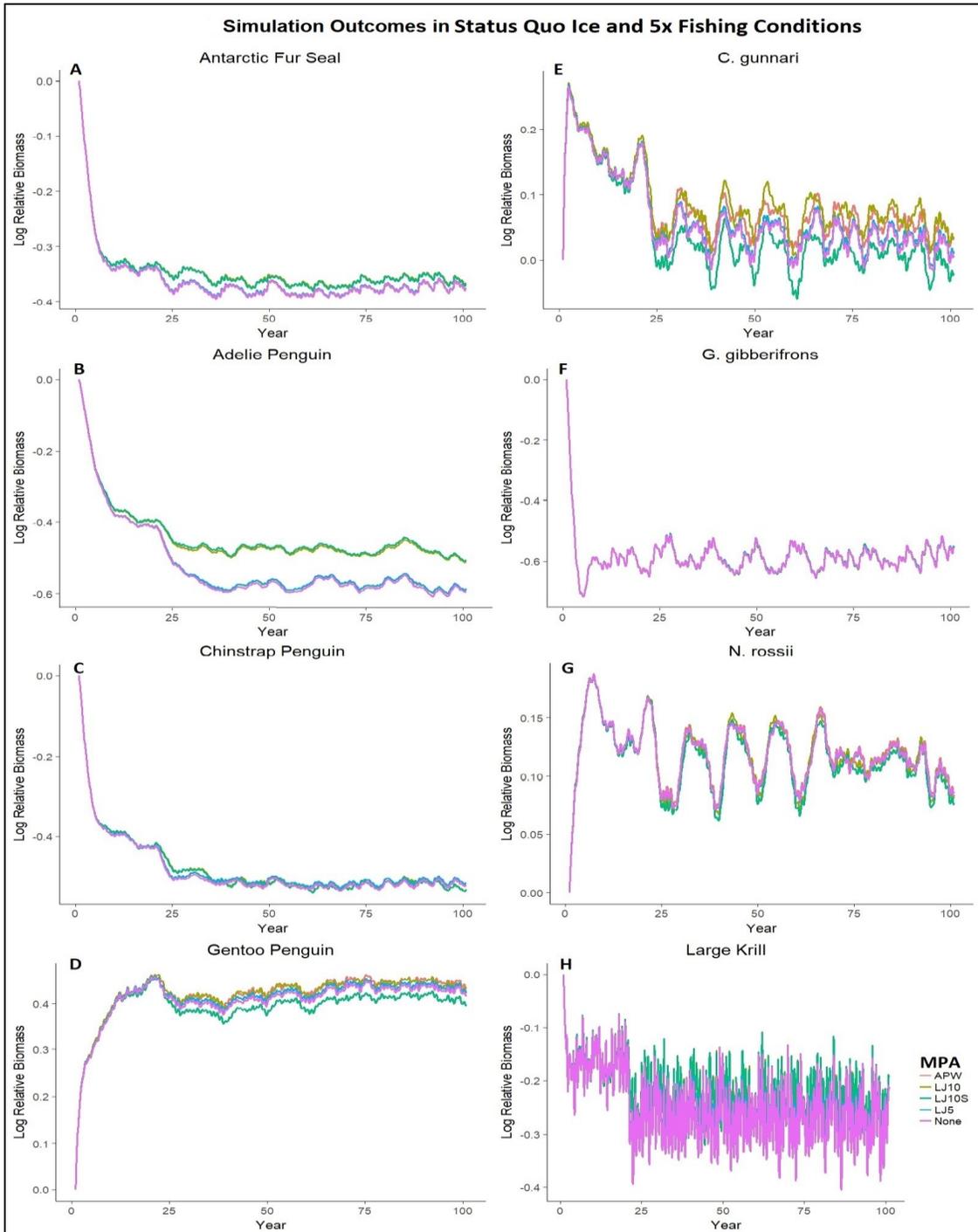


Appendix 5 xiv Spatial Outcomes for *G. gibberifrons* in Decreasing Ice conditions. Red color indicates areas of higher concentration.

Appendix 6 MPA impact on biomass outcomes in status quo ice conditions

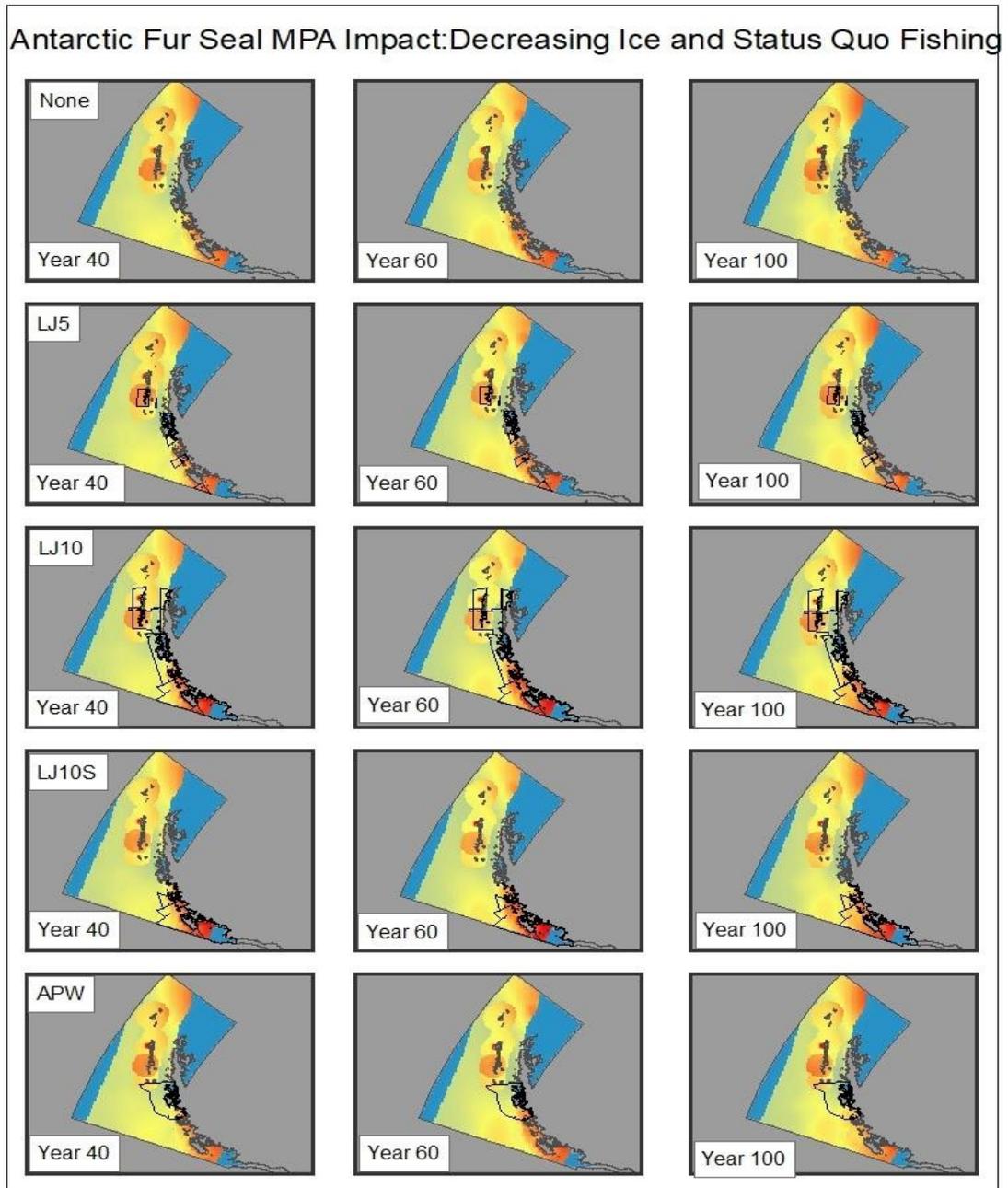


Appendix 6 i Comparison of MPA Impact at Status Quo Fishing Levels in Status Quo Ice Conditions. The LJ10 and LJ10S MPA scenarios result in slightly higher relative biomass outcomes for Antarctic fur seals (A), Adélie Penguins (B) and Krill (H).



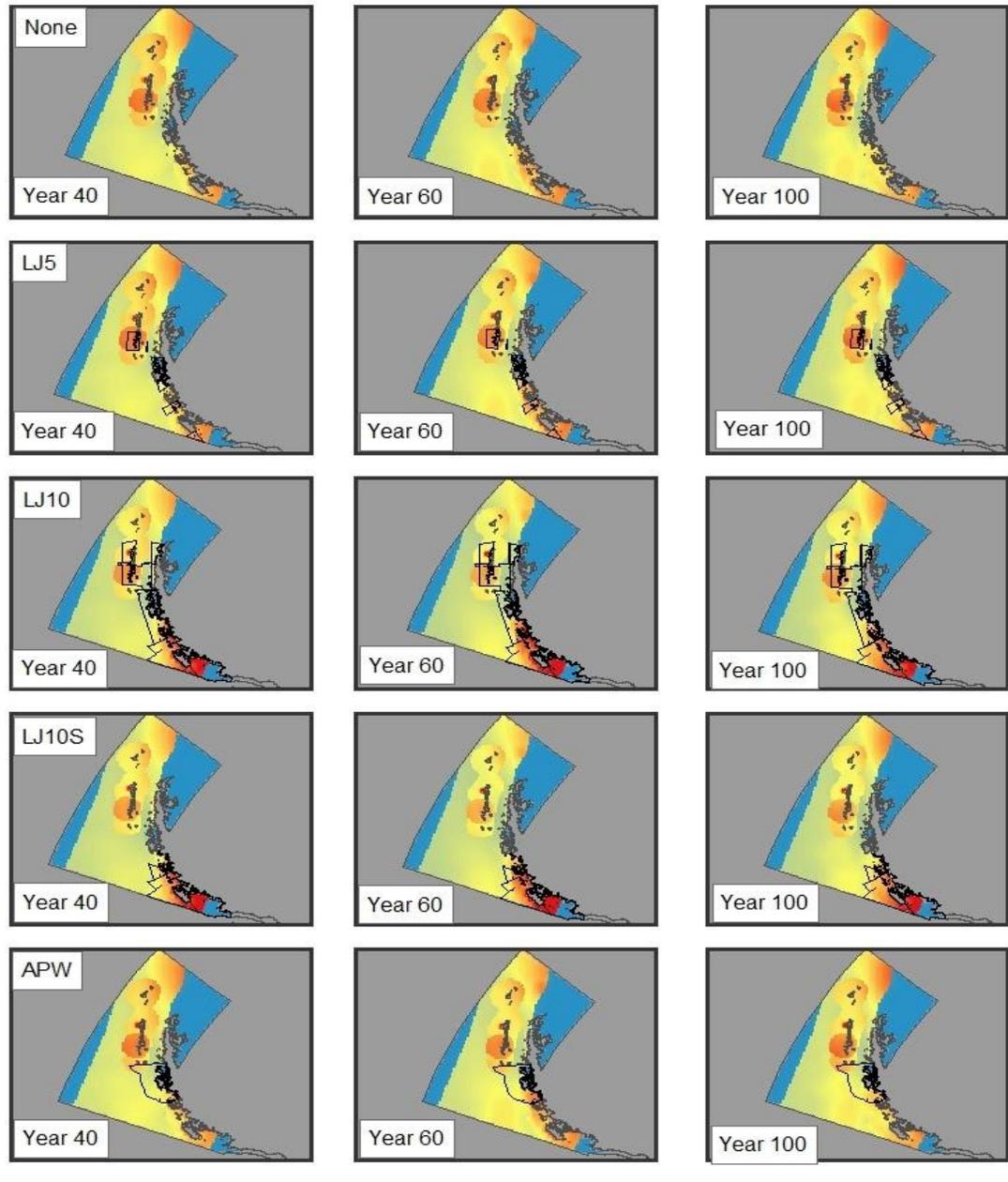
Appendix 6 ii Comparison of MPA Impact at 5x Fishing Levels in Status Quo Ice .The LJ10 and LJ10S MPA scenarios result in slightly higher relative biomass outcomes for Antarctic fur seals (A), Adélie Penguins (B) and Krill (H).

Appendix 7 Spatial outcomes across the MPA scenarios



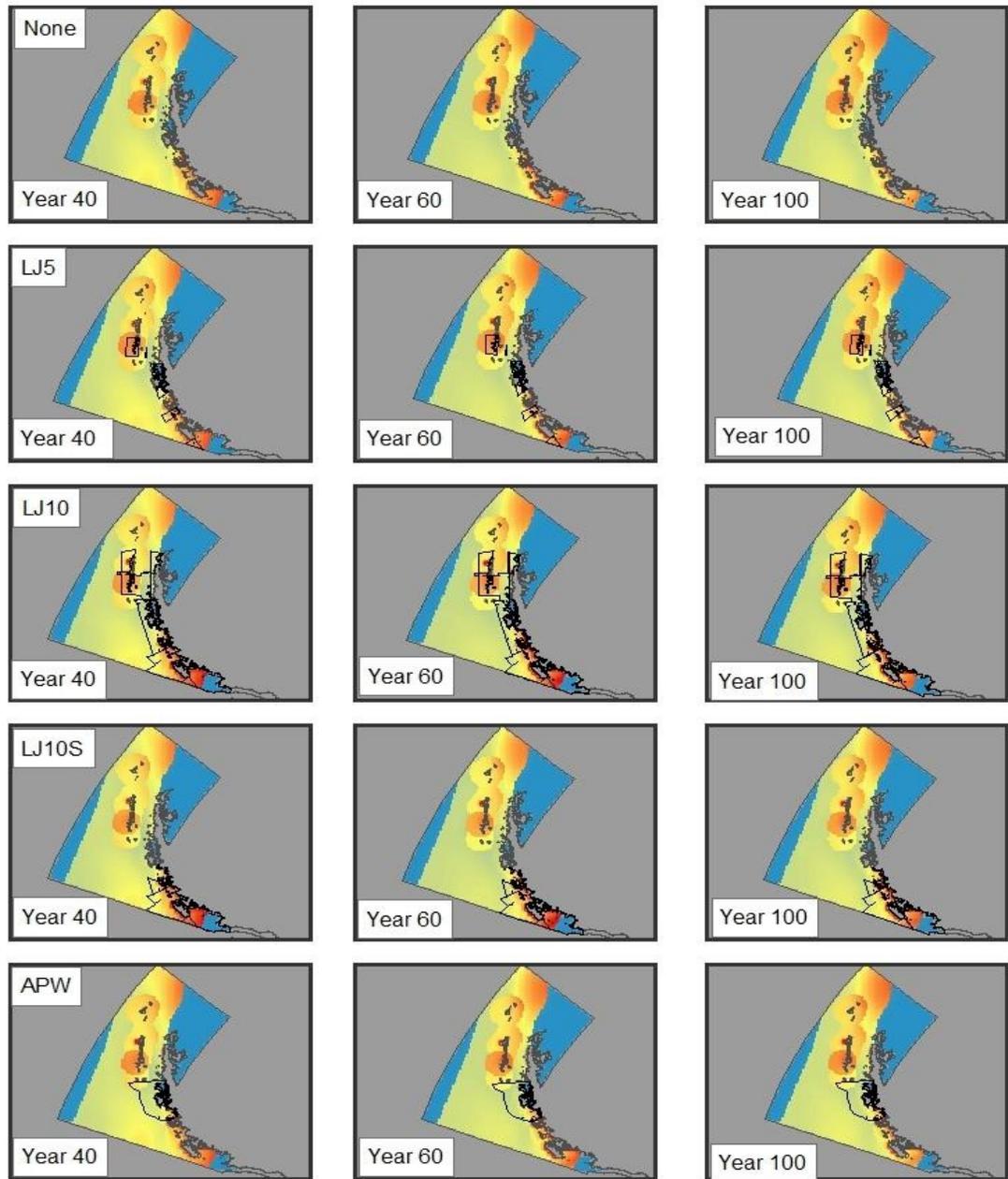
Appendix 7 i MPA impact on Antarctic fur seal in Decreasing Ice Scenario Under Status Quo Fishing Pressure. Red color indicates areas of greater concentration.

Antarctic Fur Seal MPA Impact: Decreasing Ice and 5x Fishing



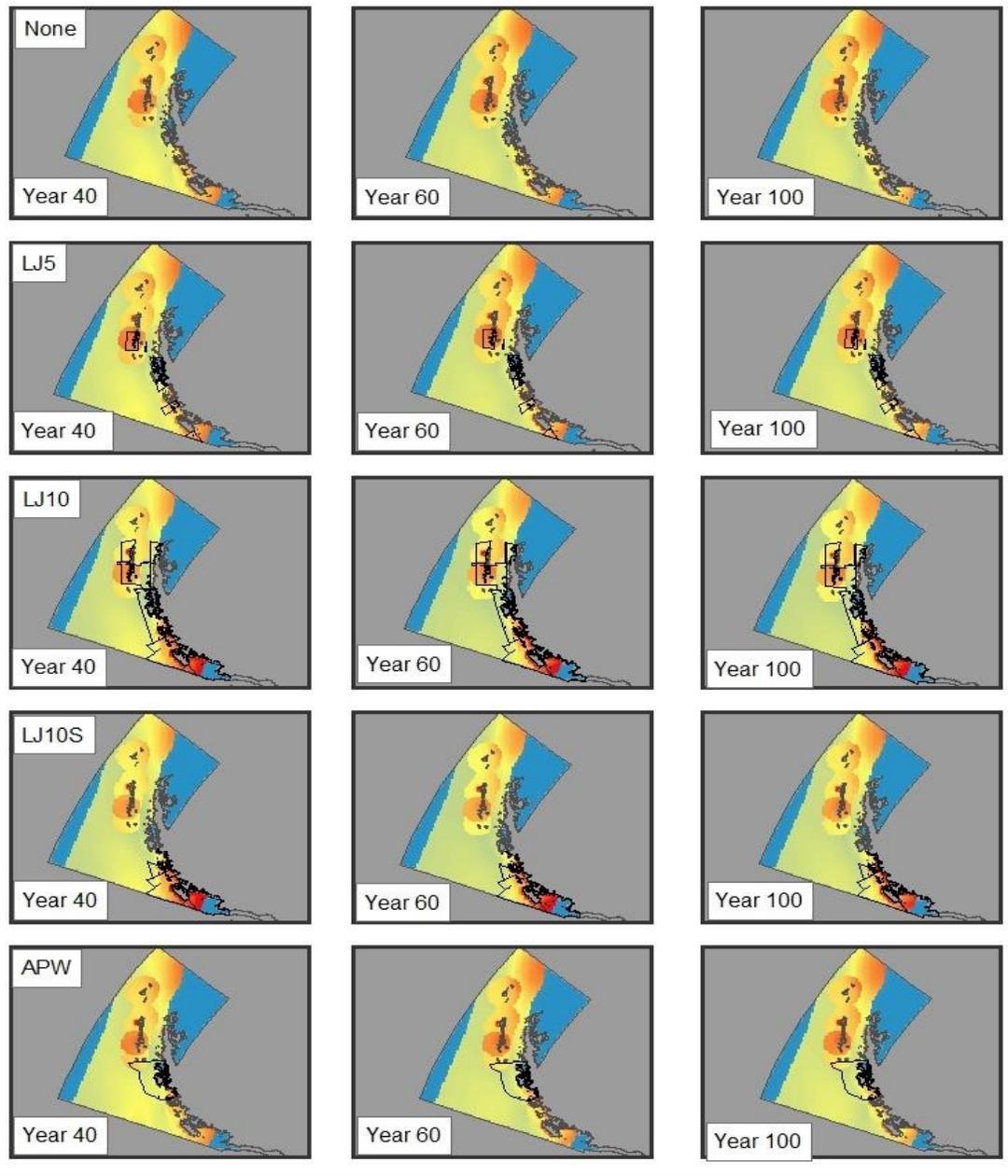
Appendix 7 ii MPA impact on Antarctic fur seal in Decreasing Ice Scenario Under 5x Fishing Pressure. Red color indicates areas of greater concentration.

Antarctic Fur Seal MPA Impact: Status Quo Ice and Status Quo Fishing



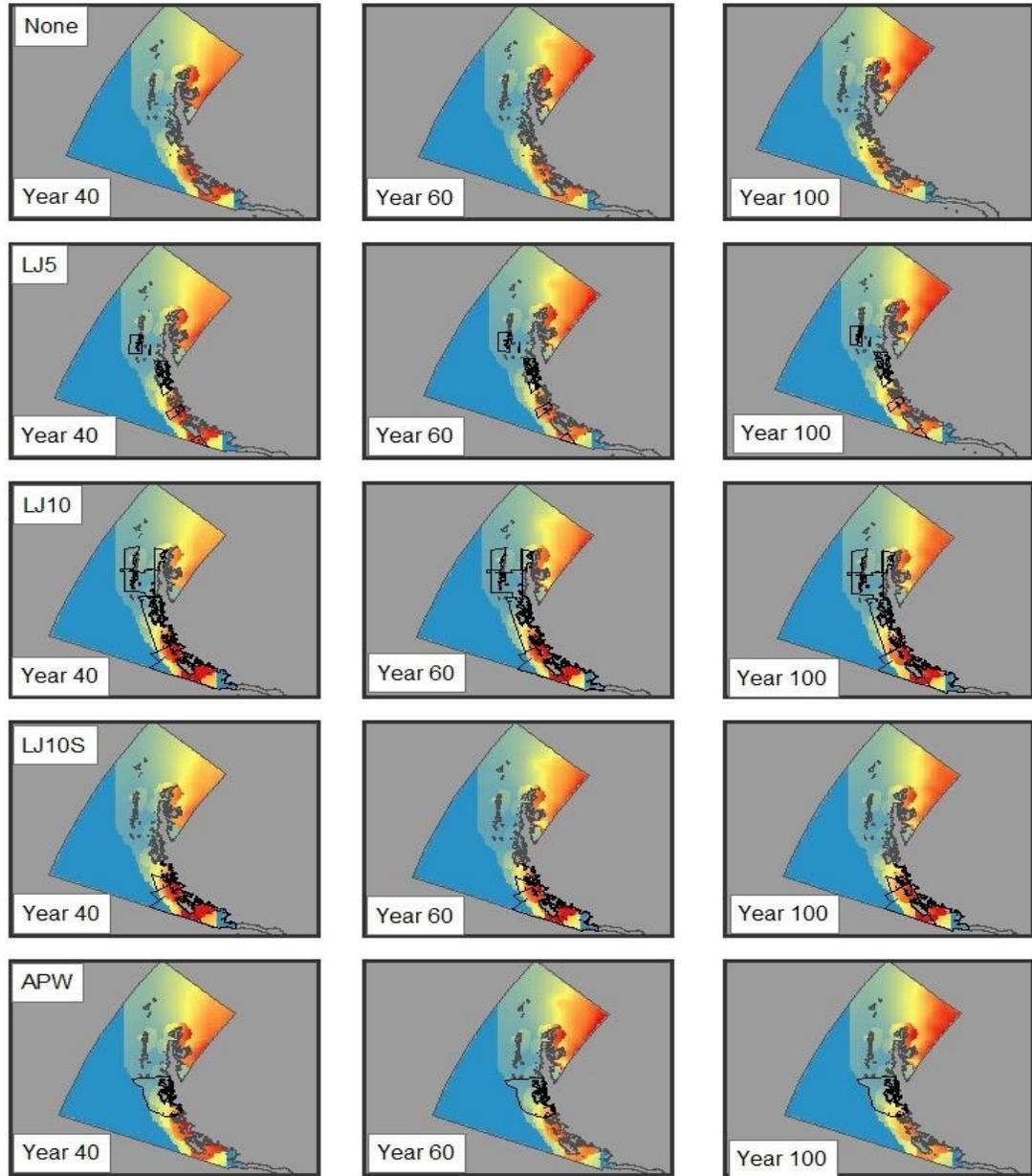
Appendix 7 iii MPA impact on Antarctic fur seal in Status Quo Ice Scenario Under Status Quo Fishing Pressure. Red color indicates areas of greater concentration.

Antarctic Fur Seal MPA Impact: Status Quo Ice and 5x Fishing



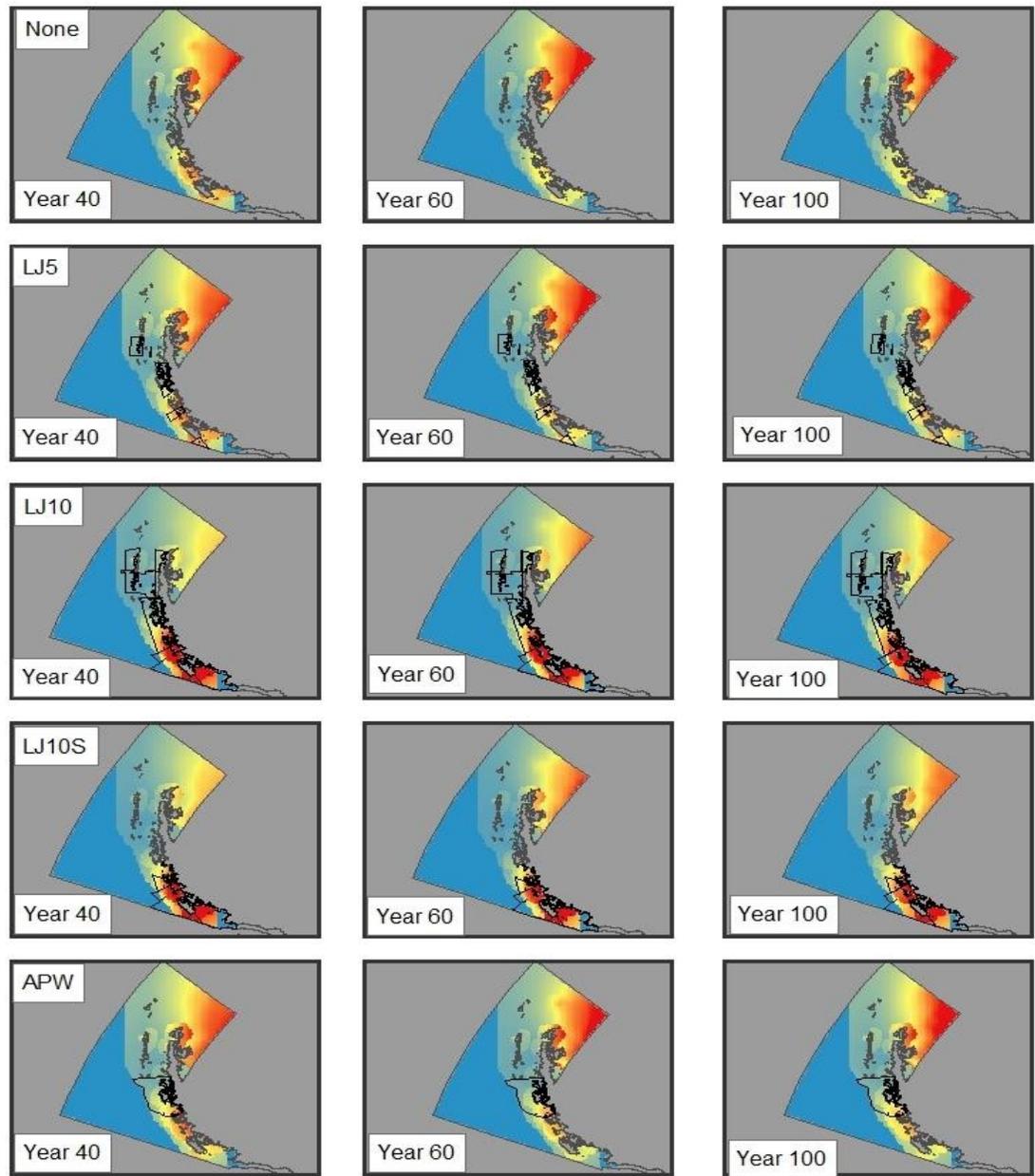
Appendix 7 iv MPA impact on Antarctic fur seal in Status Quo Ice Scenario Under 5x Fishing Pressure. Red color indicates areas of greater concentration.

Adelie Penguin MPA Impact: Decreasing Ice and SQ Fishing



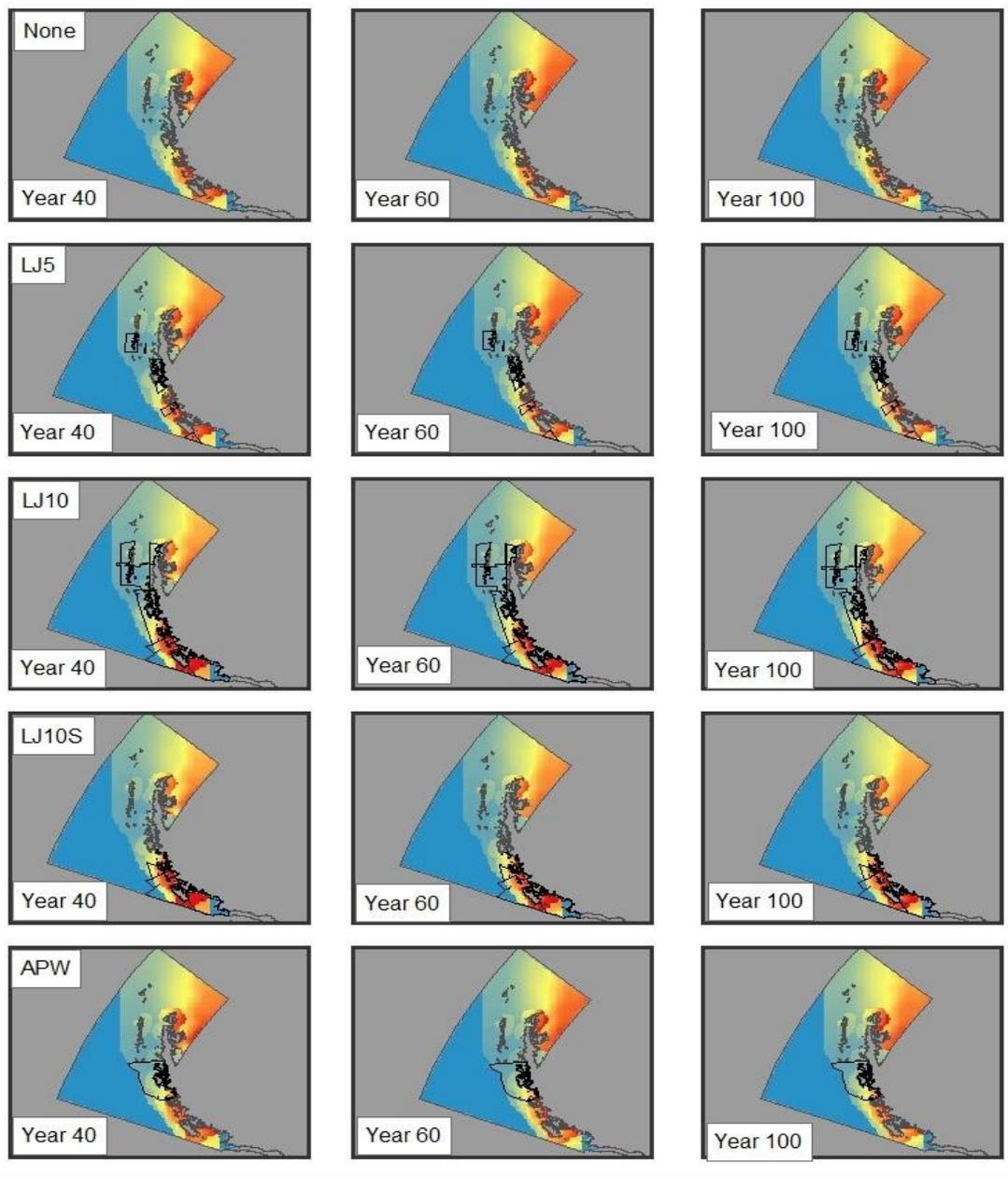
Appendix 7 v MPA impact on Adélie Penguin in Decreasing Ice Scenario Under Status Quo Fishing Pressure. Red color indicates areas of greater concentration.

Adelie Penguin MPA Impact: Decreasing Ice and 5x Fishing



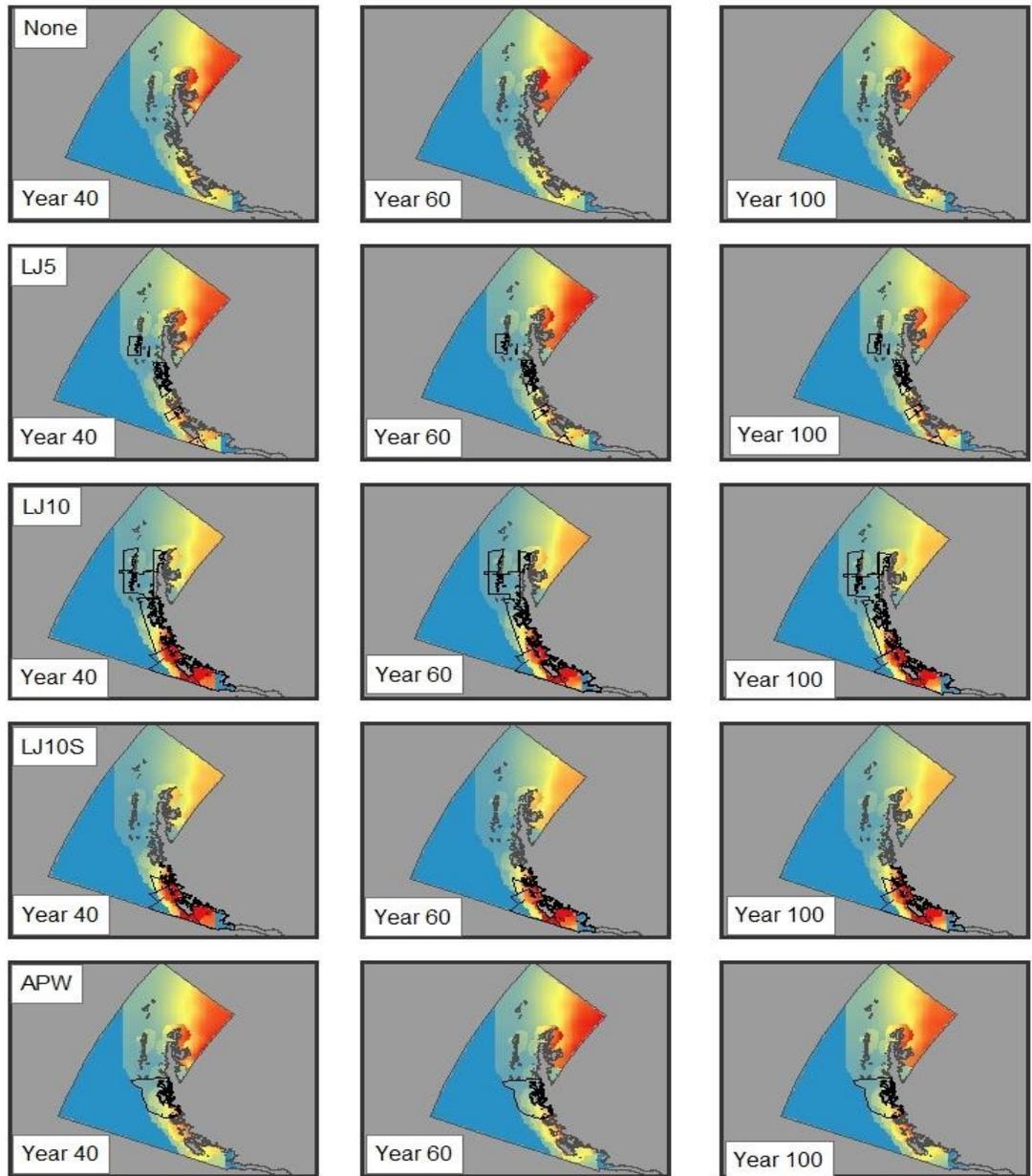
Appendix 7 vi MPA impact on Adélie Penguin in Decreasing Ice Scenario Under Status Quo Fishing Pressure. Red color indicates areas of greater concentration.

Adelie Penguin MPA Impact: Status Quo Ice and Status Quo Fishing



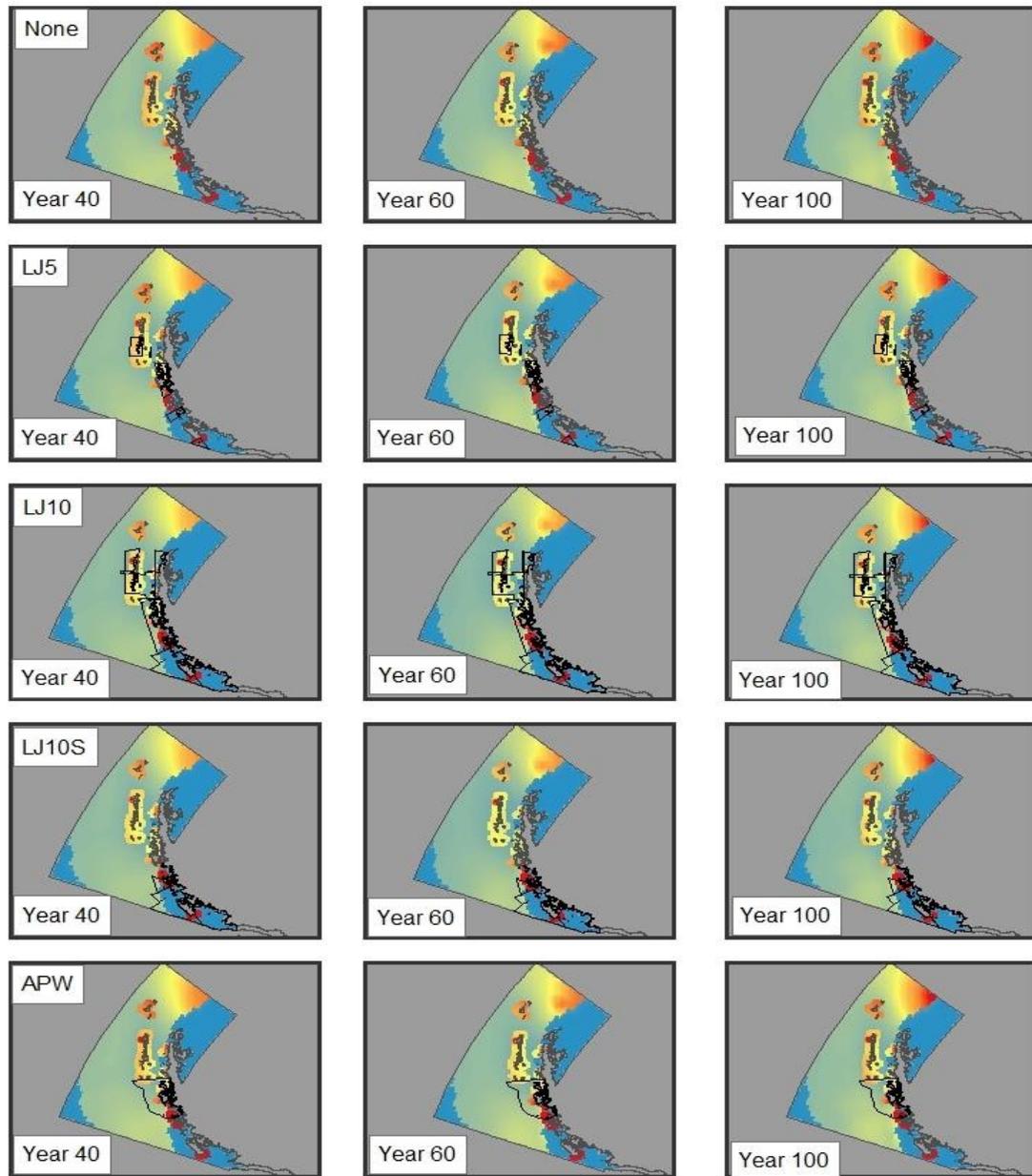
Appendix 7 vii MPA impact on Adélie Penguins in Status Quo Ice Scenario Under Status Quo Fishing Pressure. Red color indicates areas of greater concentration.

Adelie Penguin MPA Impact: Status Quo Ice and 5x Fishing



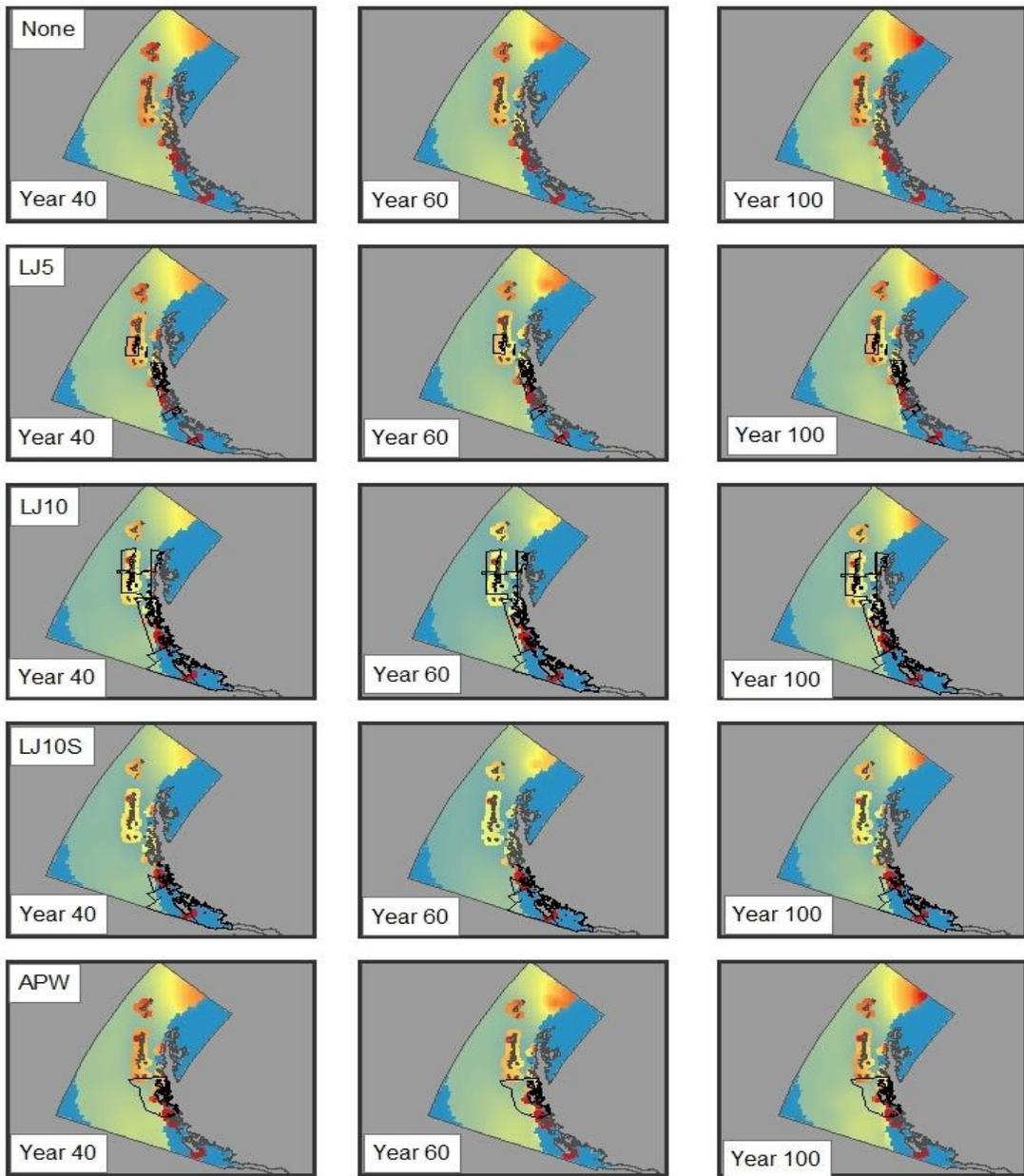
Appendix 7 viii MPA impact on Adélie Penguins in Status Quo Ice Scenario Under 5x Fishing Pressure. Red color indicates areas of greater concentration.

Chinstrap Penguin MPA Impact: Decreasing Ice and Status Quo Fishing



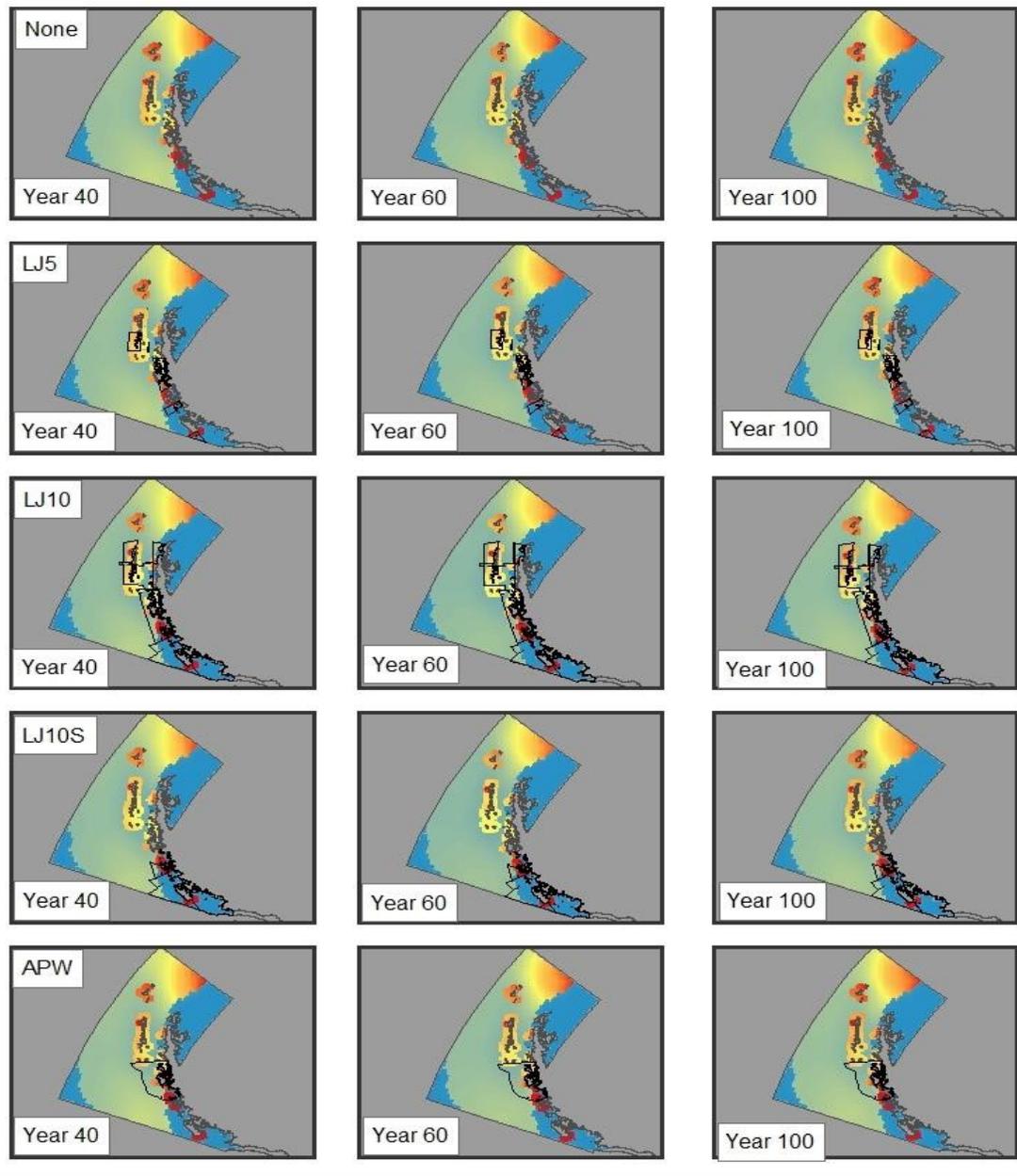
Appendix 7 ix Chinstrap Penguins in Decreasing Ice Scenario Under Status Quo Fishing Pressure. Red color indicates areas of greater concentration.

Chinstrap Penguin MPA Impact: Decreasing Ice and 5x Fishing

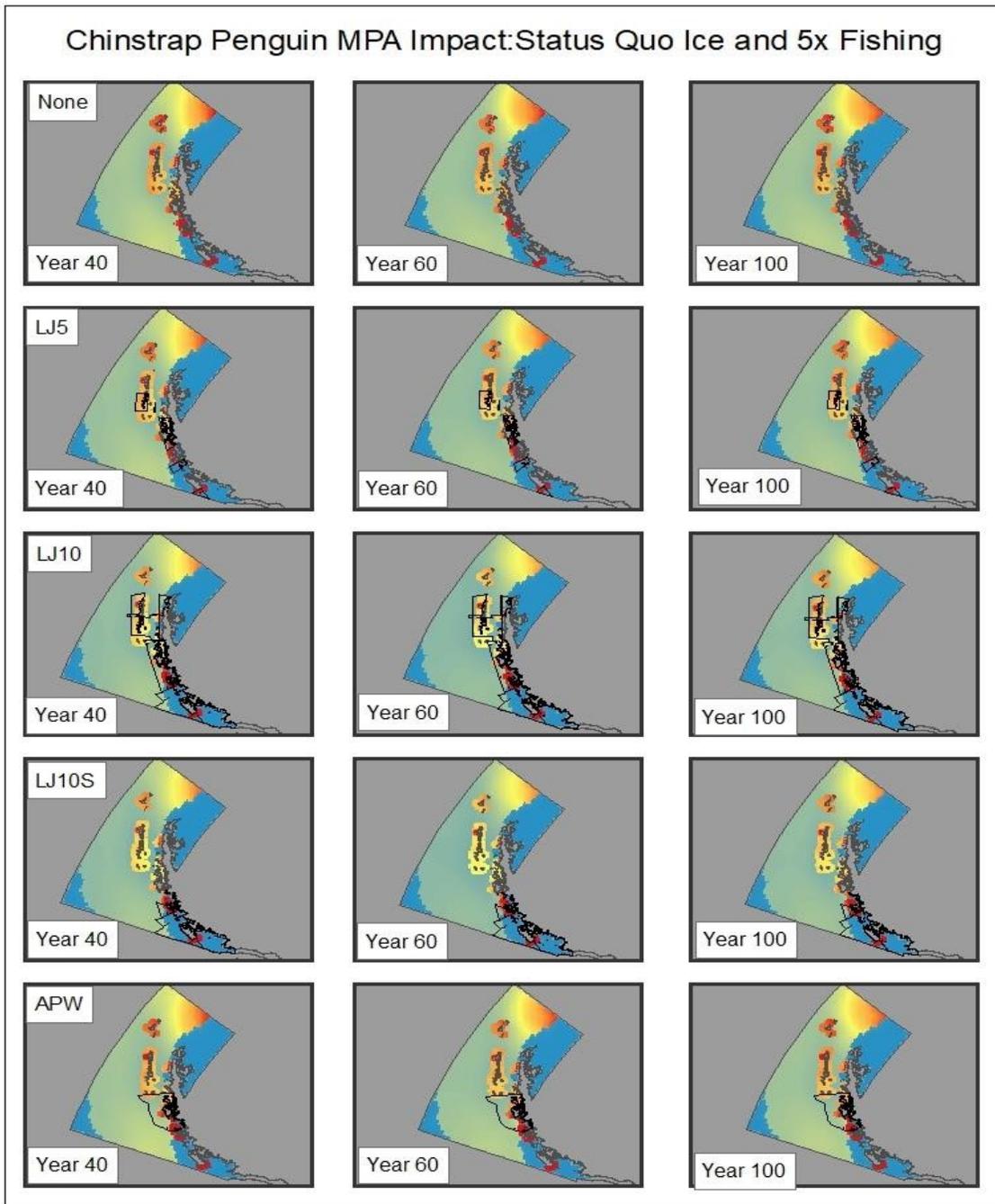


Appendix 7 x Chinstrap Penguins in Decreasing Ice Scenario Under 5x Fishing Pressure. Red color indicates areas of greater concentration.

Chinstrap Penguin MPA Impact: Status Quo Ice and Status Quo Fishing

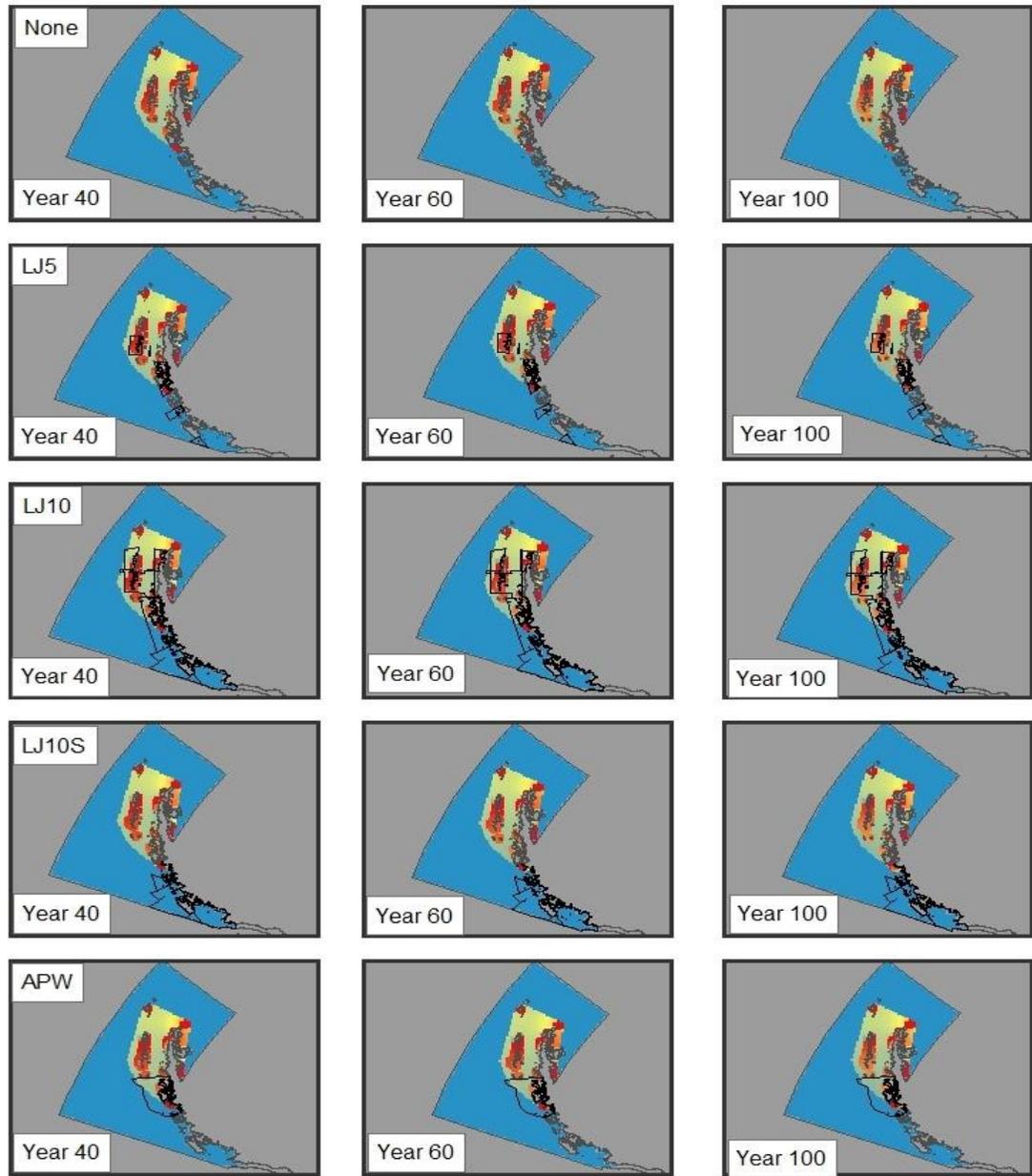


Appendix 7 xi Chinstrap Penguins in Status Quo Ice Scenario Under Status Quo Fishing Pressure. Red color indicates areas of greater concentration.



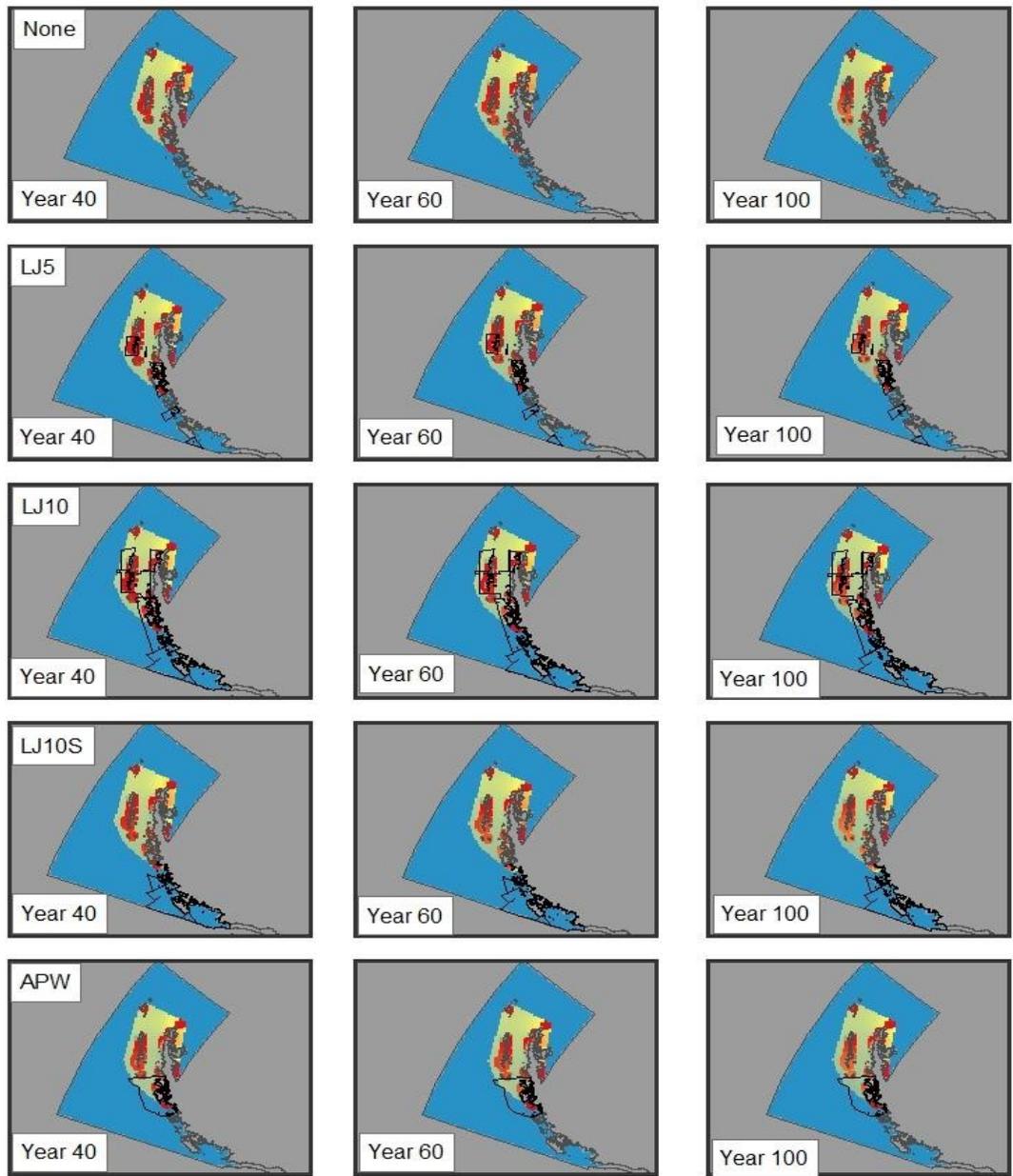
Appendix 7 xii Chinstrap Penguins in Status Quo Ice Scenario Under 5x Fishing Pressure. Red color indicates areas of greater concentration.

Gentoo Penguin MPA Impact: Decreasing Ice and Status Quo Fishing



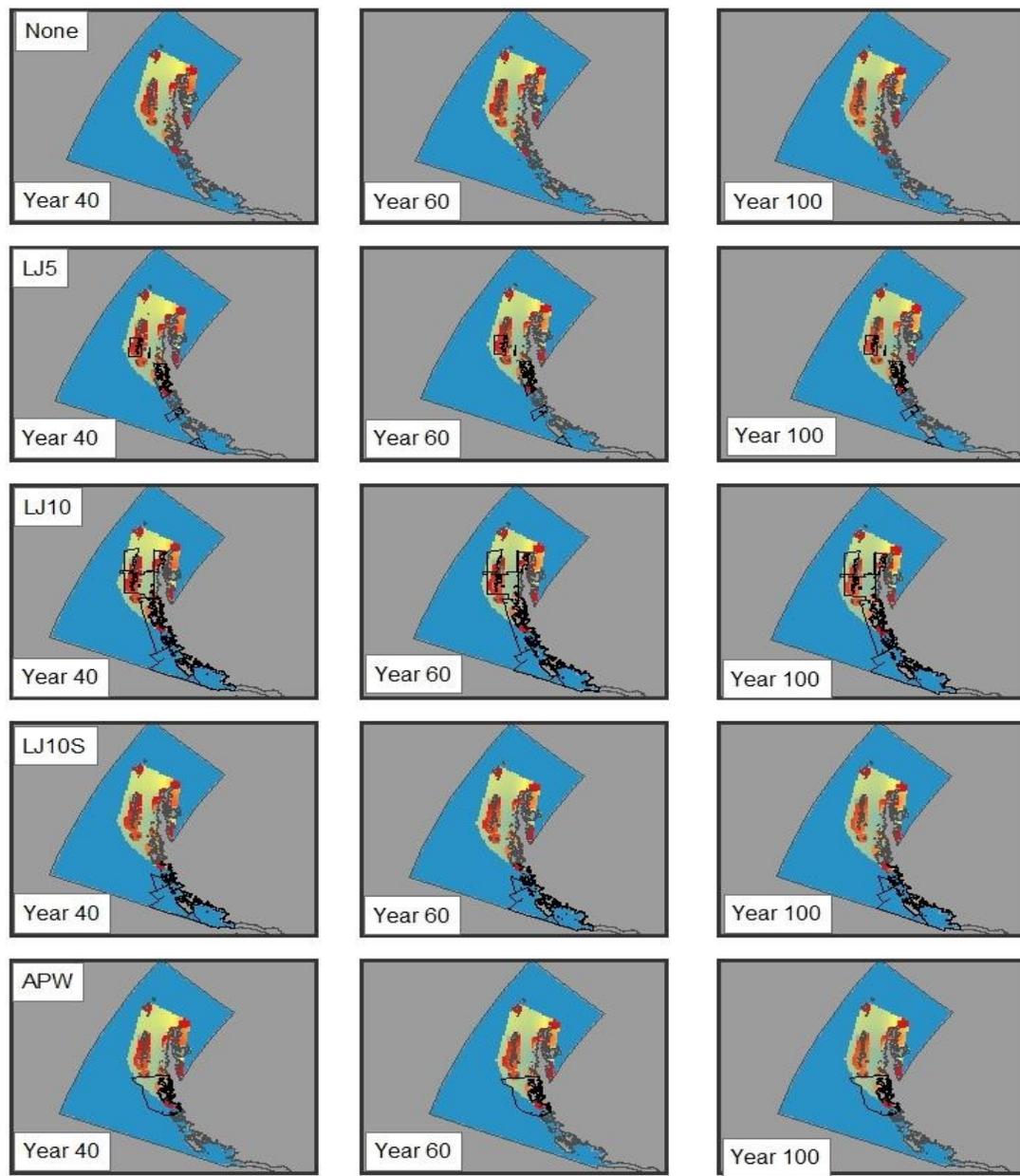
Appendix 7 xiii Gentoo Penguins in Decreasing Ice Scenario Under Status Quo Fishing Pressure. Red color indicates areas of greater concentration.

Gentoo Penguin MPA Impact: Decreasing Ice and 5x Fishing



Appendix 7 xiv Gentoo Penguins in Decreasing Ice Scenario Under 5x Fishing Pressure. Red color indicates areas of greater concentration.

Gentoo Penguin MPA Impact: Status Quo Ice and Status Quo Fishing

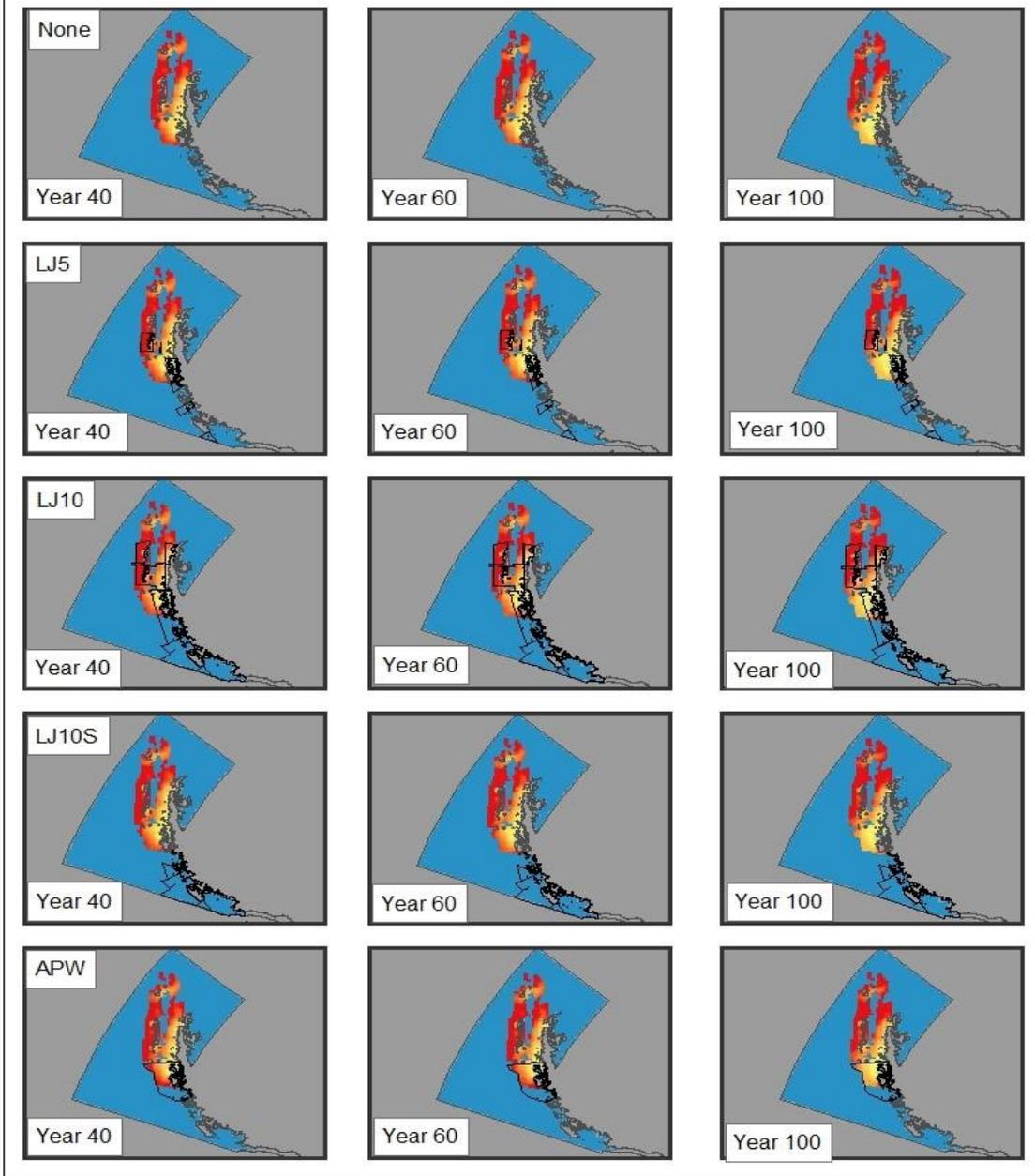


Appendix 7 xv Gentoo Penguins in Status Quo Ice Scenario under Status Quo Fishing. Pressure Red color indicates areas of greater concentration.



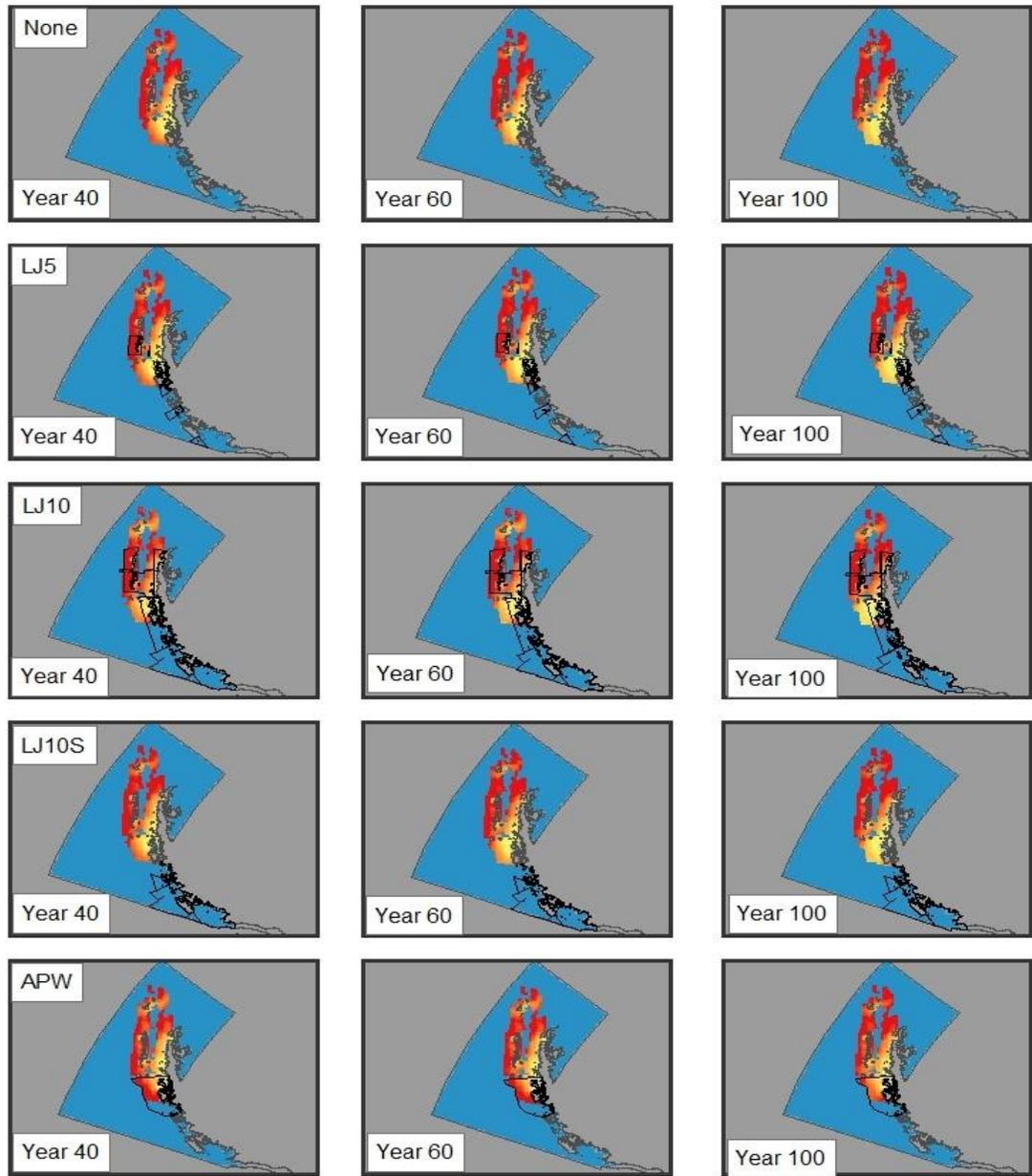
Appendix 7 xvi Gentoo Penguins in Status Quo Ice Scenario under 5x Fishing Pressure. Red color indicates areas of greater concentration.

C. gunnari MPA Impact: Decreasing Ice and Status Quo Fishing



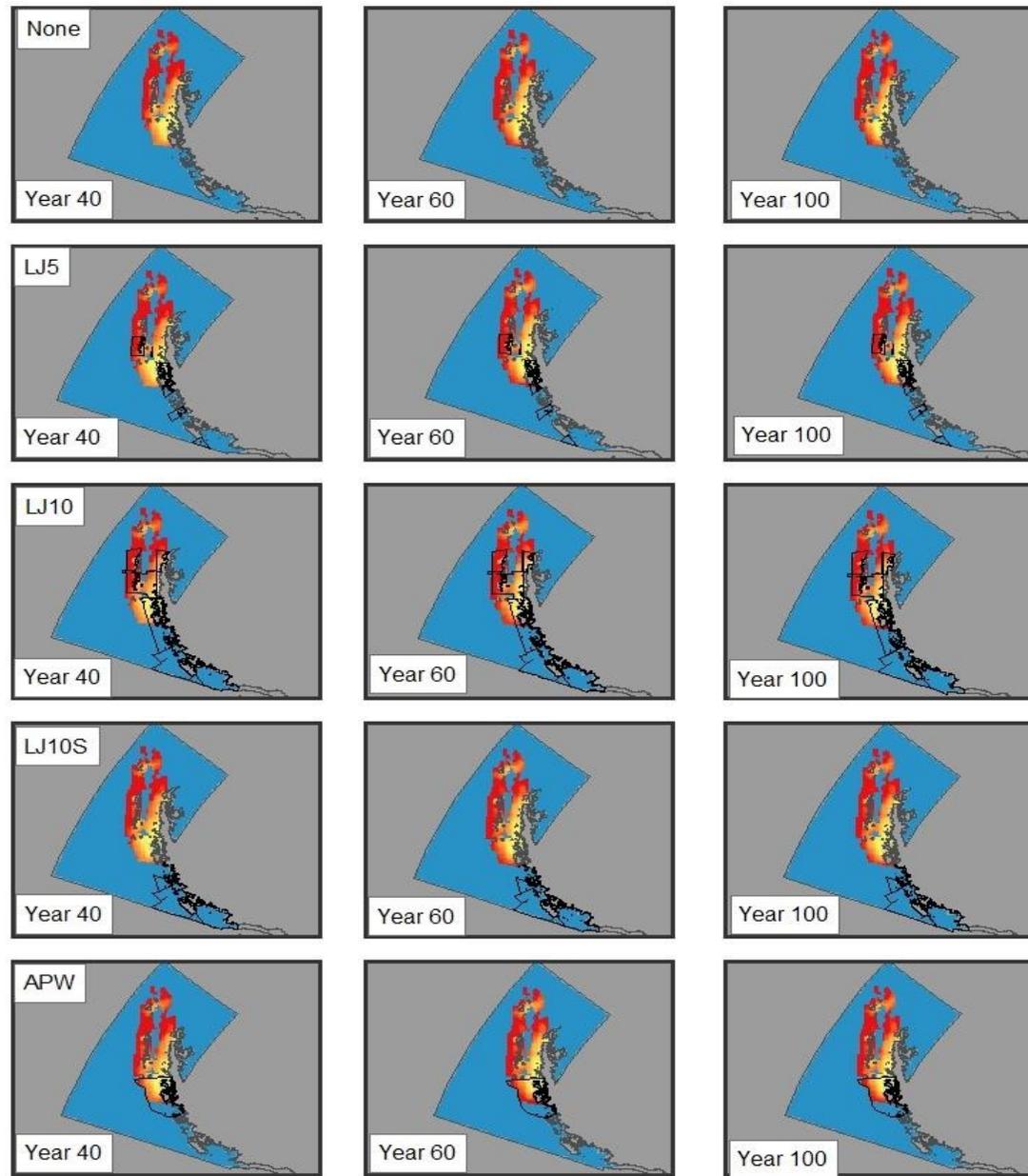
Appendix 7 xvii *C. gunnari* in Decreasing Ice Scenario under Status Quo Fishing Pressure. Red color indicates areas of greater concentration.

C. gunnari MPA Impact: Decreasing Ice and 5x Fishing



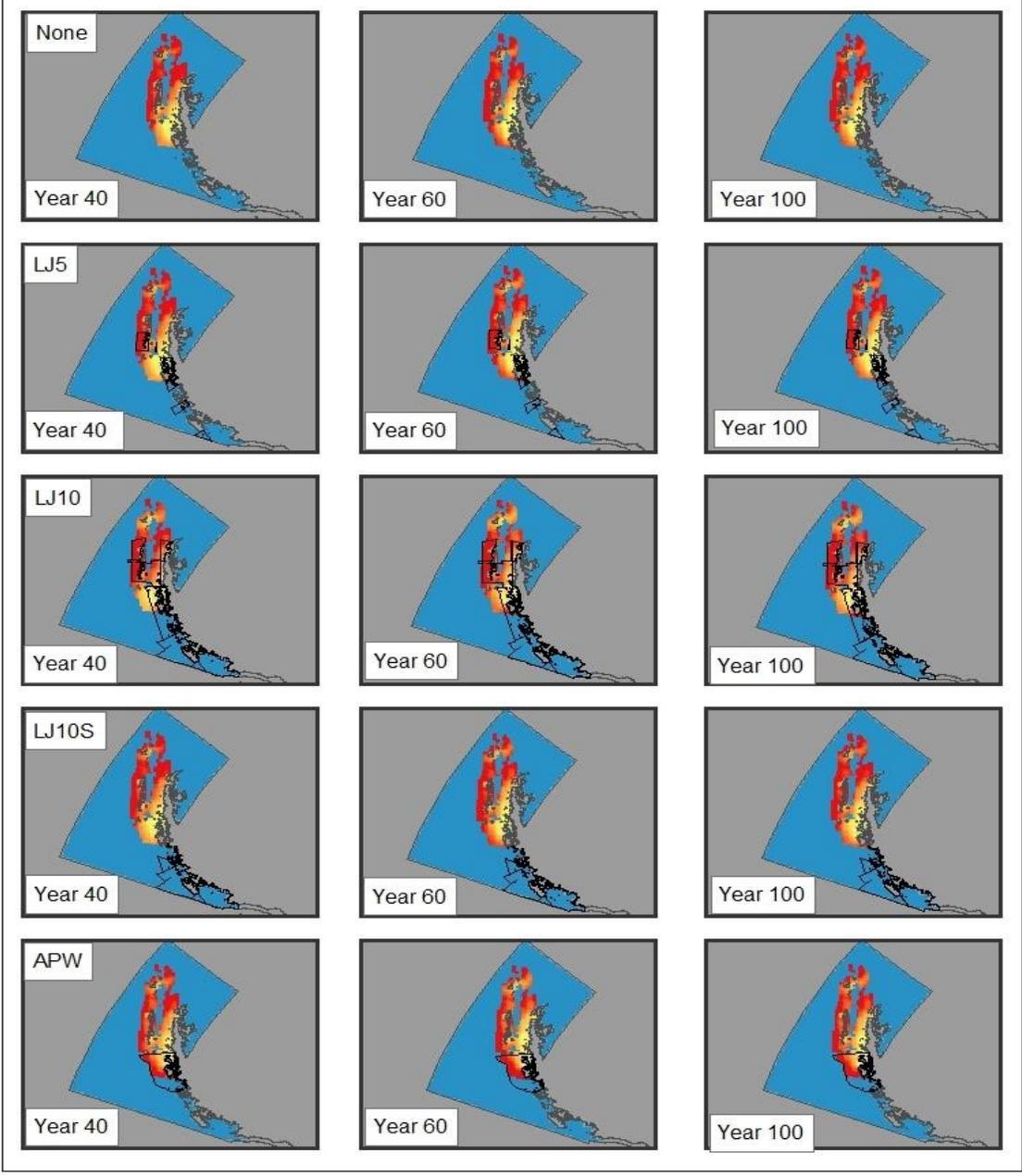
Appendix 7 xviii *C. gunnari* in Decreasing Ice Scenario under 5x Fishing Pressure. Red color indicates areas of greater concentration.

C. gunnari MPA Impact: Status Quo Ice and Status Quo Fishing



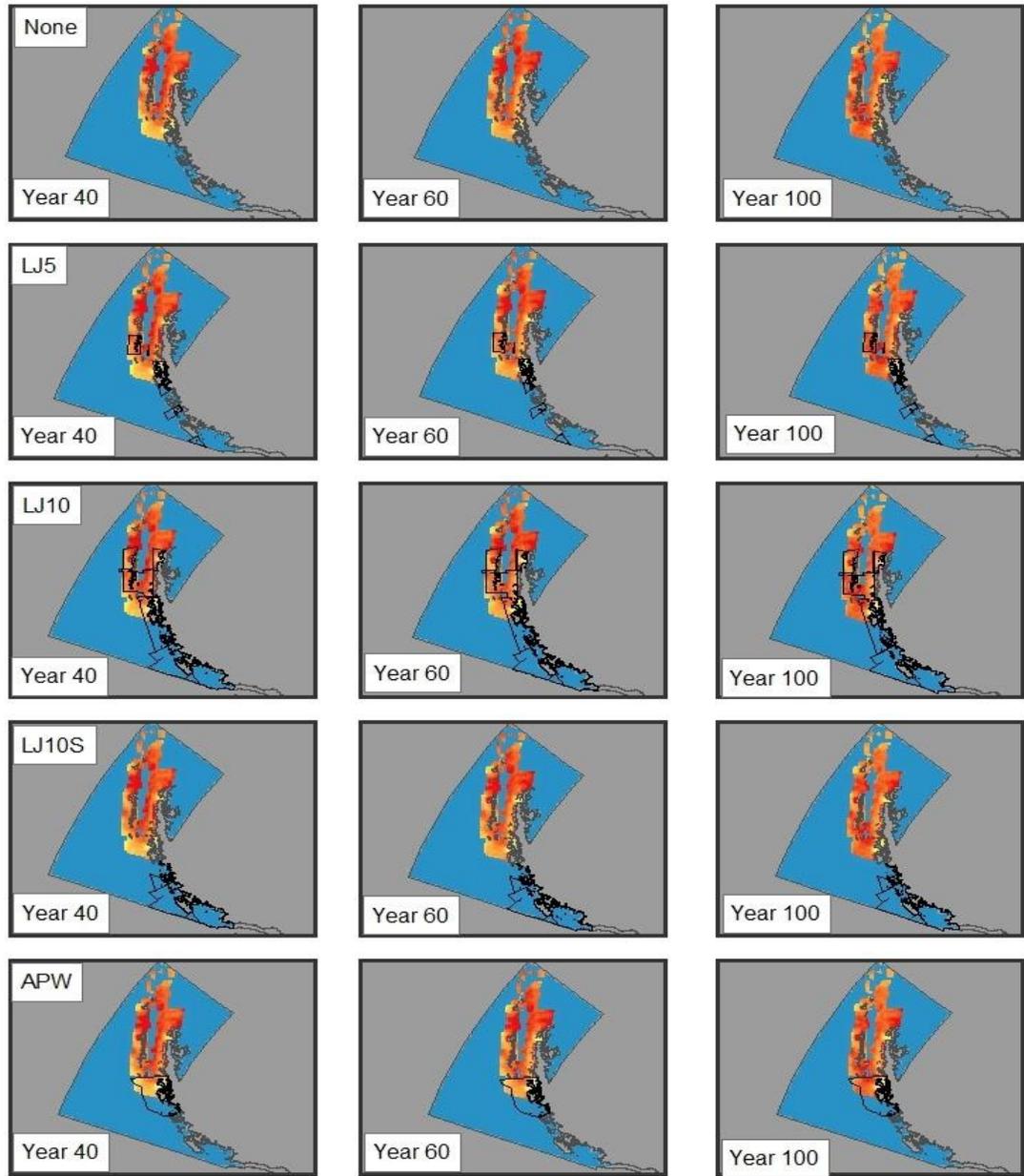
Appendix 7 xix *C. gunnari* in Status Quo Ice Scenario under Status Quo Fishing Pressure. Red color indicates areas of greater concentration.

C. gunnari MPA Impact: Status Quo Ice and 5x Fishing



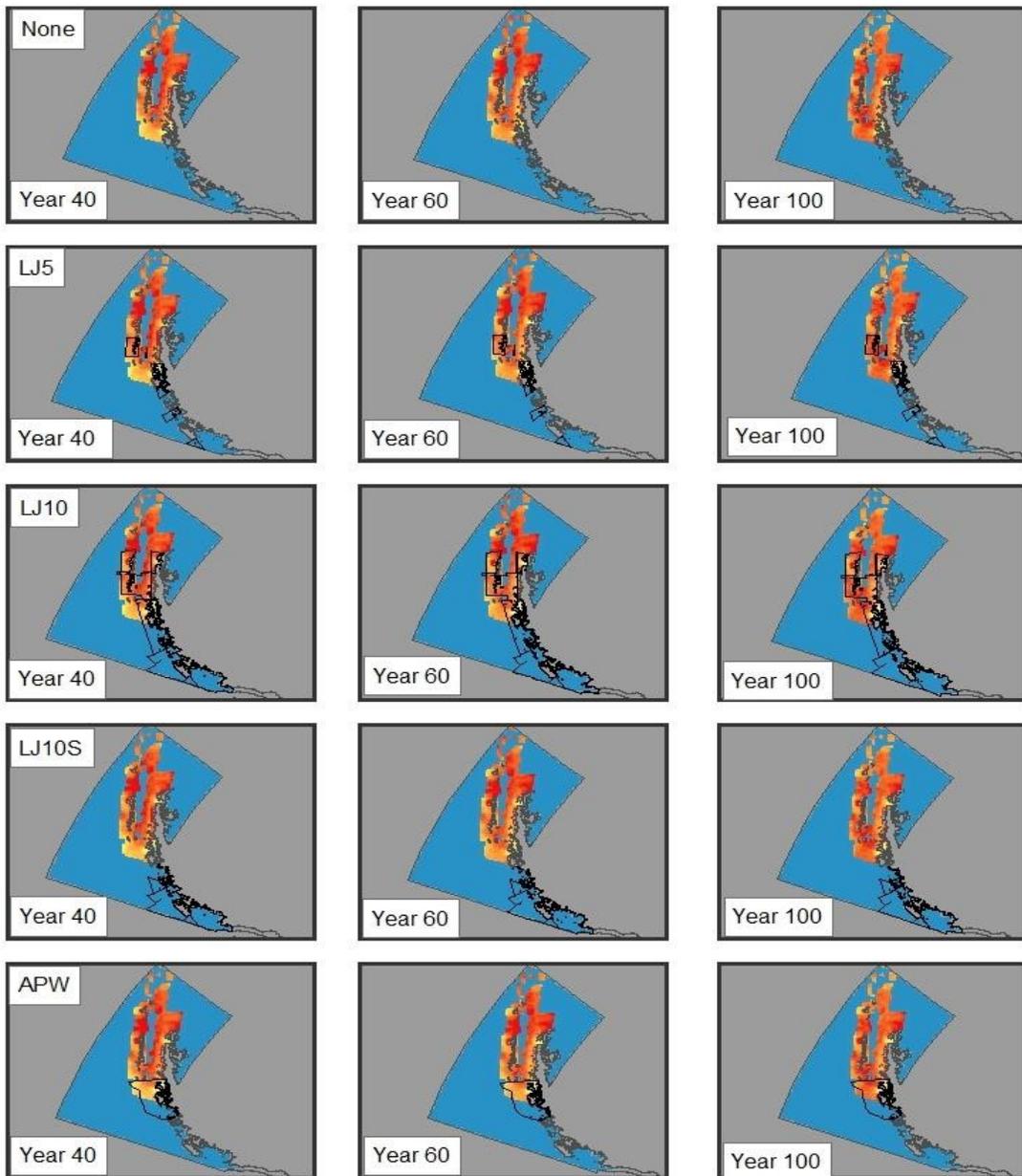
Appendix 7 xx *C. gunnari* in Status Quo Ice Scenario under 5x Fishing Pressure. Red color indicates areas of greater concentration.

G. gibberifrons MPA Impact: Decreasing Ice and Status Quo Fishing



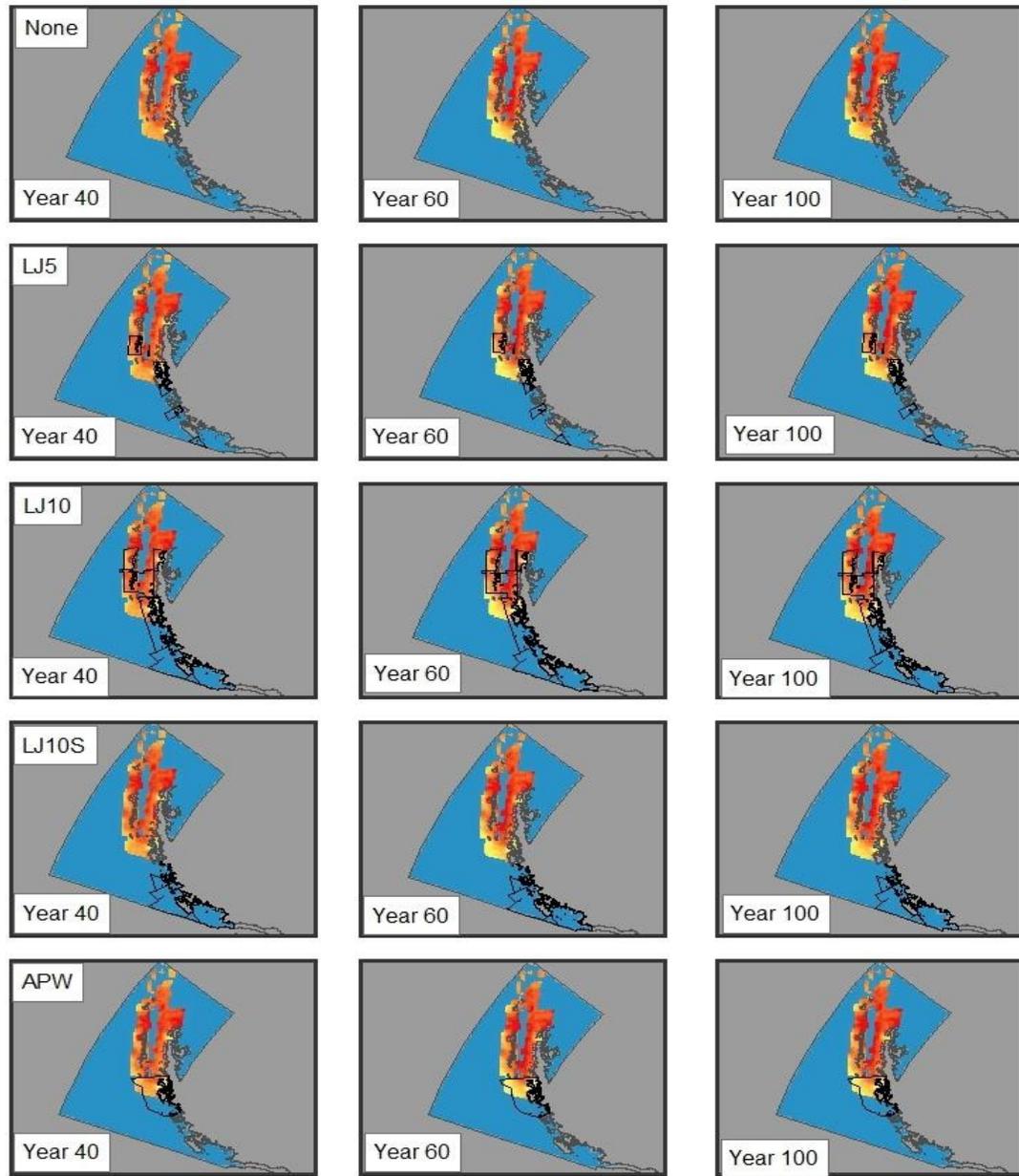
Appendix 7 xxi *G. gibberifrons* in Decreasing Ice Scenario under Status Quo Fishing Pressure. Red color indicates areas of greater concentration.

G. gibberifrons MPA Impact: Decreasing Ice and 5x Fishing



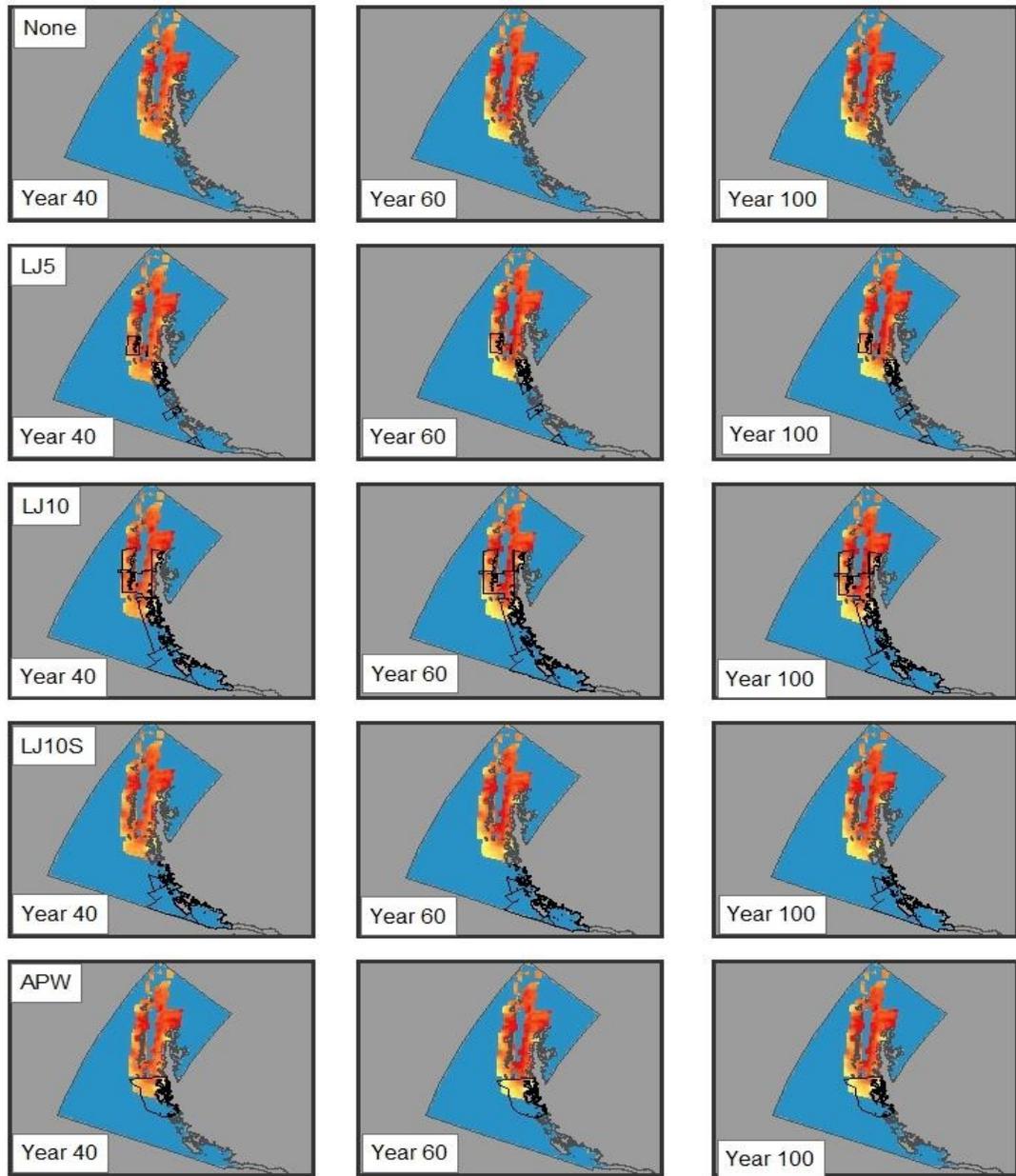
Appendix 7 xxii *G. gibberifrons* in Decreasing Ice Scenario under 5x Fishing Pressure. Red color indicates areas of greater concentration.

G. gibberifrons MPA Impact: Status Quo Ice and Status Quo Fishing

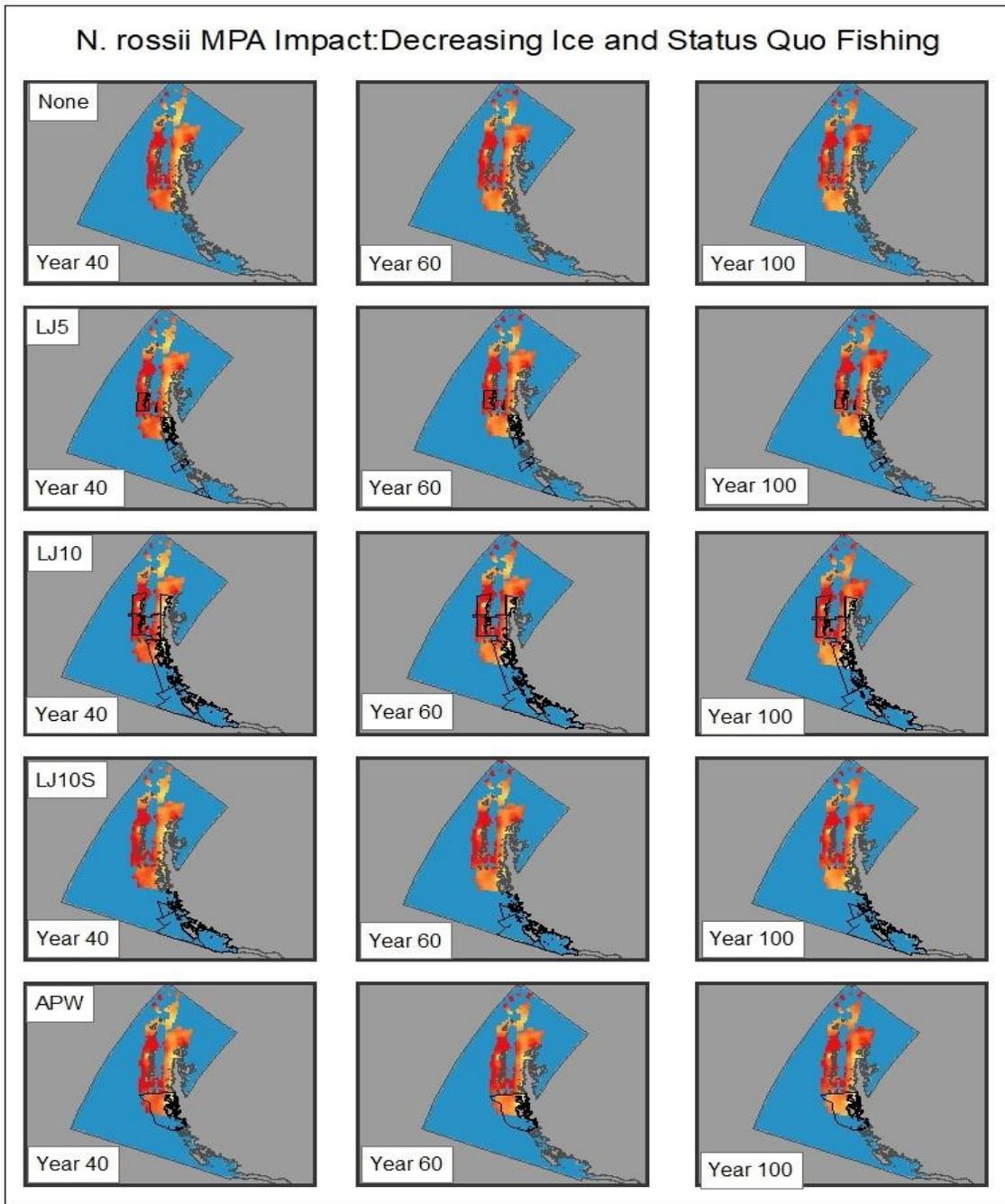


Appendix 7 xxiii *G. gibberifrons* in Status Quo Ice Scenario under Status Quo Fishing Pressure. Red color indicates areas of greater concentration.

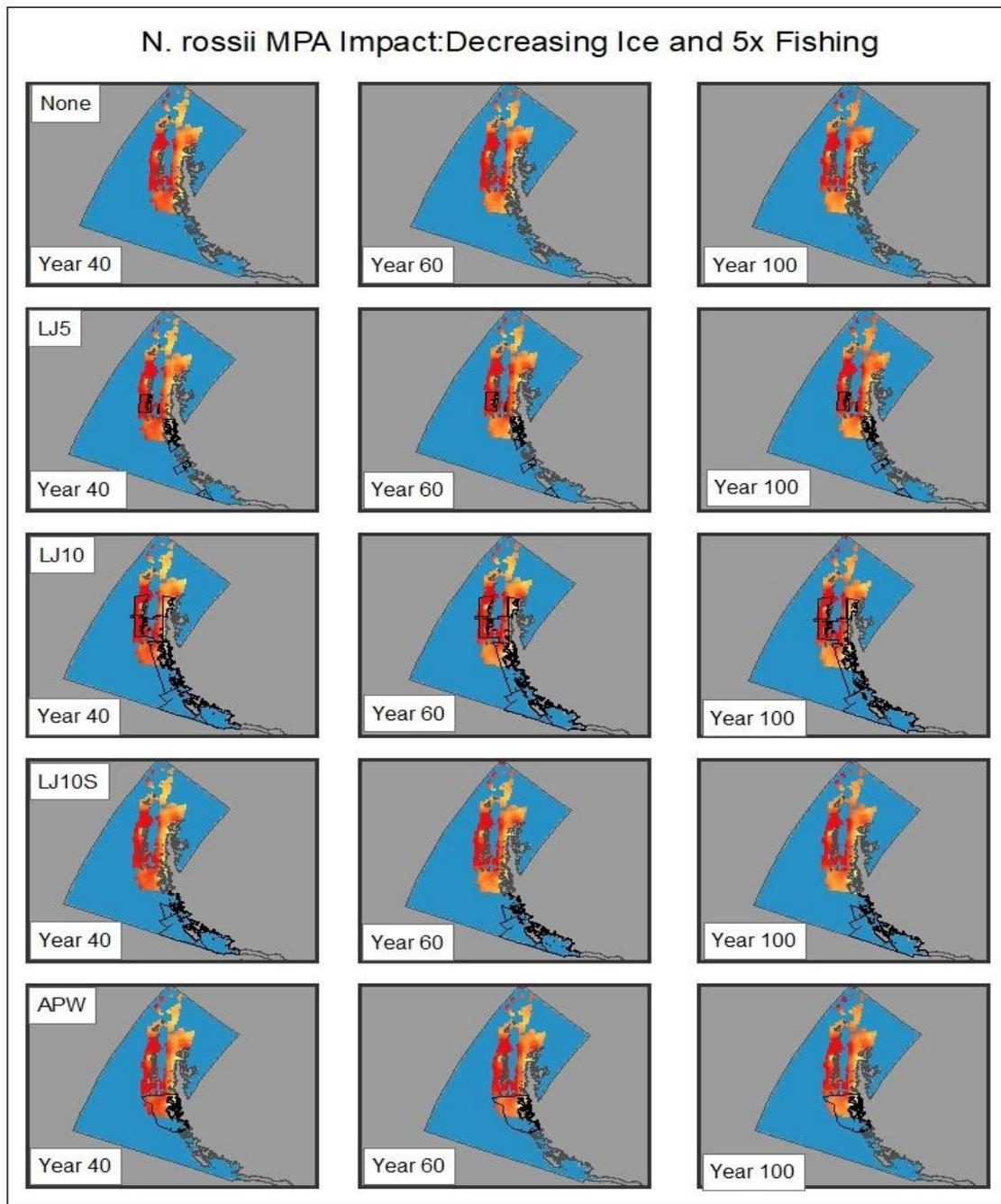
G. gibberifrons MPA Impact: Status Quo Ice and 5x Fishing



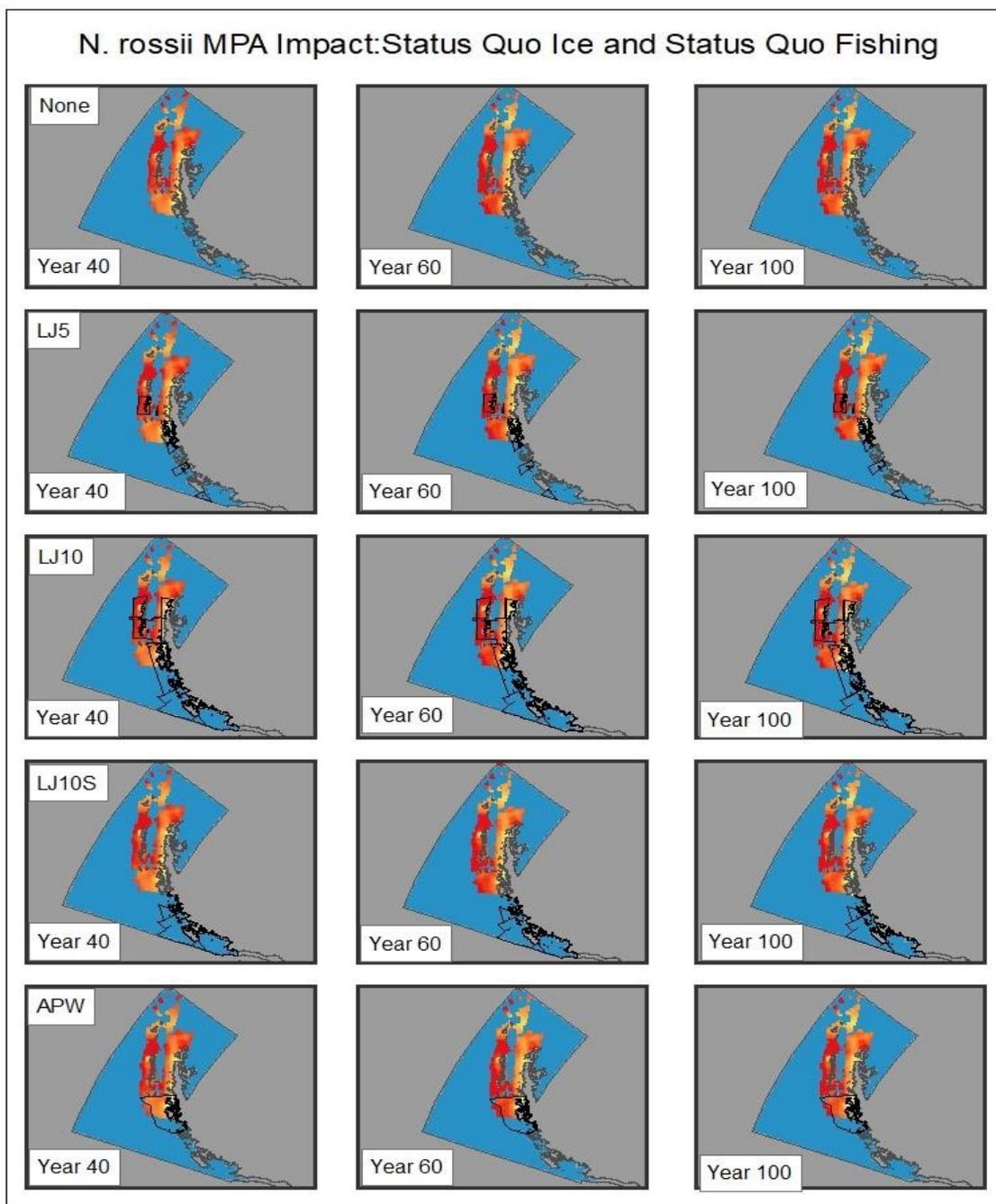
Appendix 7 xxiv *G. gibberifrons* in Status Quo Ice Scenario under 5x Fishing Pressure. Red color indicates areas of greater concentration.



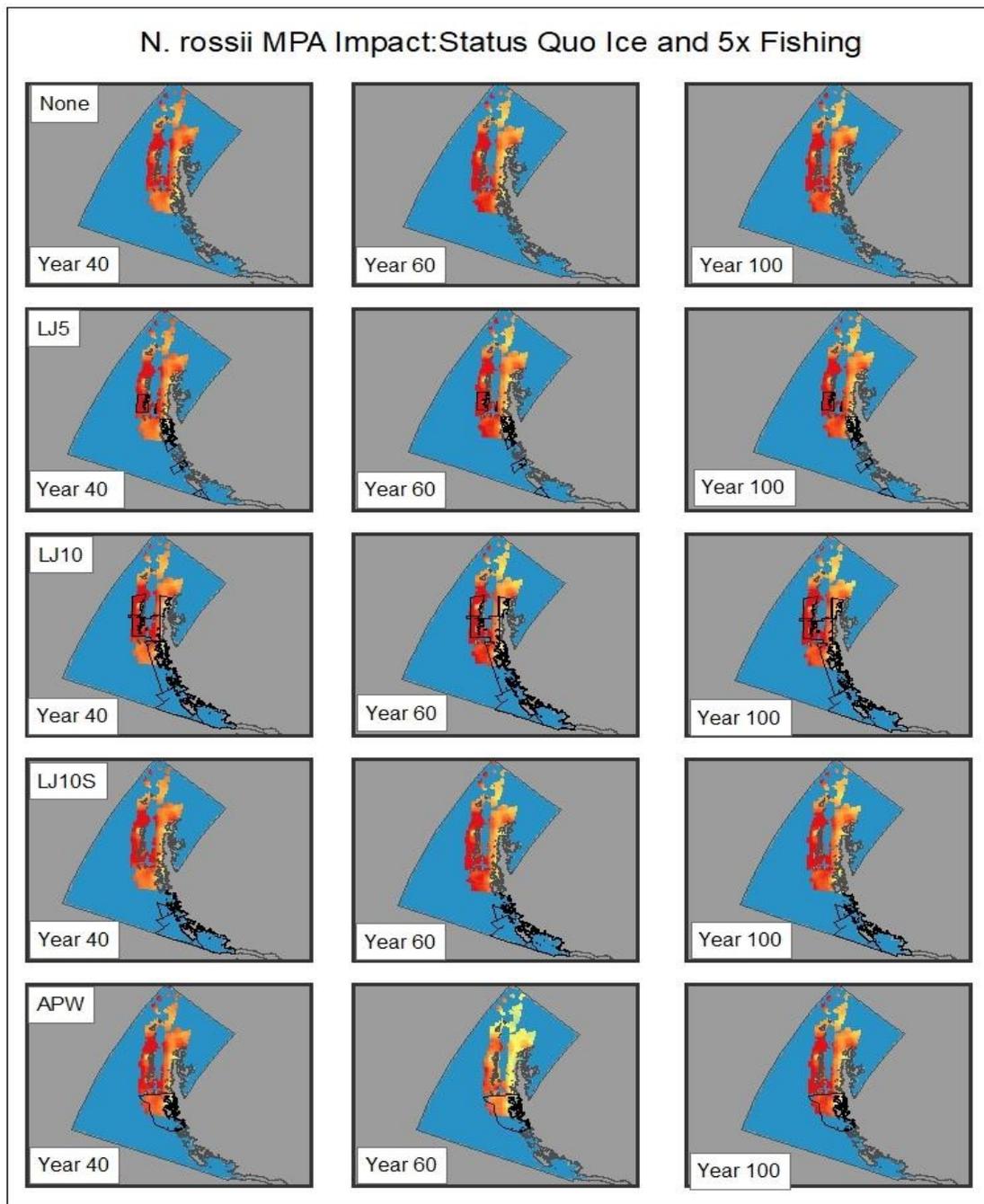
Appendix 7 xxv *N. rossii* in Decreasing Ice Scenario under Status Quo Fishing Pressure. Red color indicates areas of greater concentration.



Appendix 7 xxvi *N. rossii* in Decreasing Ice Scenario under 5x Fishing Pressure. Red color indicates areas of greater concentration.

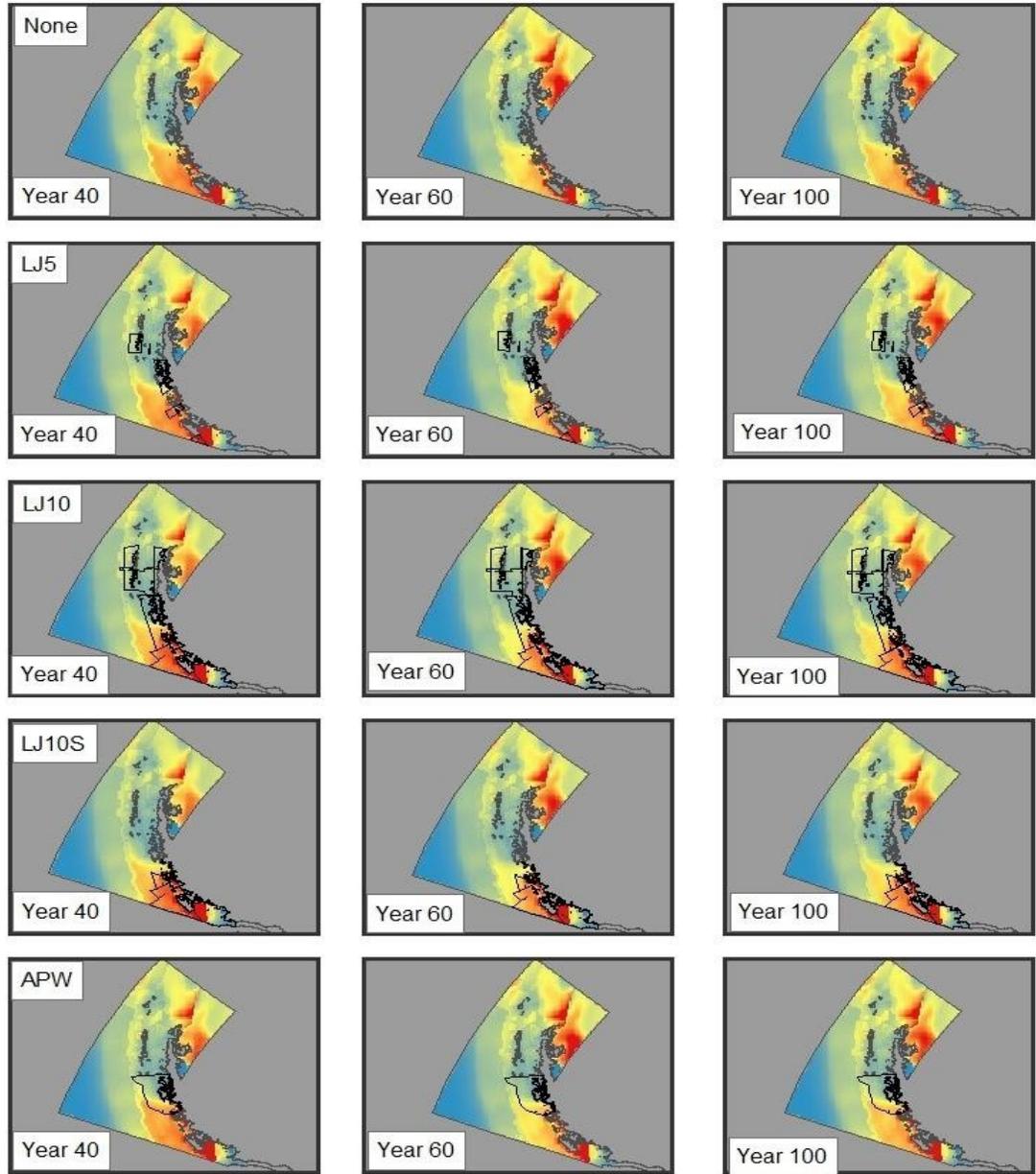


Appendix 7 xviii *N. rossii* in Status Quo Ice Scenario under Status Quo Fishing Pressure. Red color indicates areas of greater concentration.

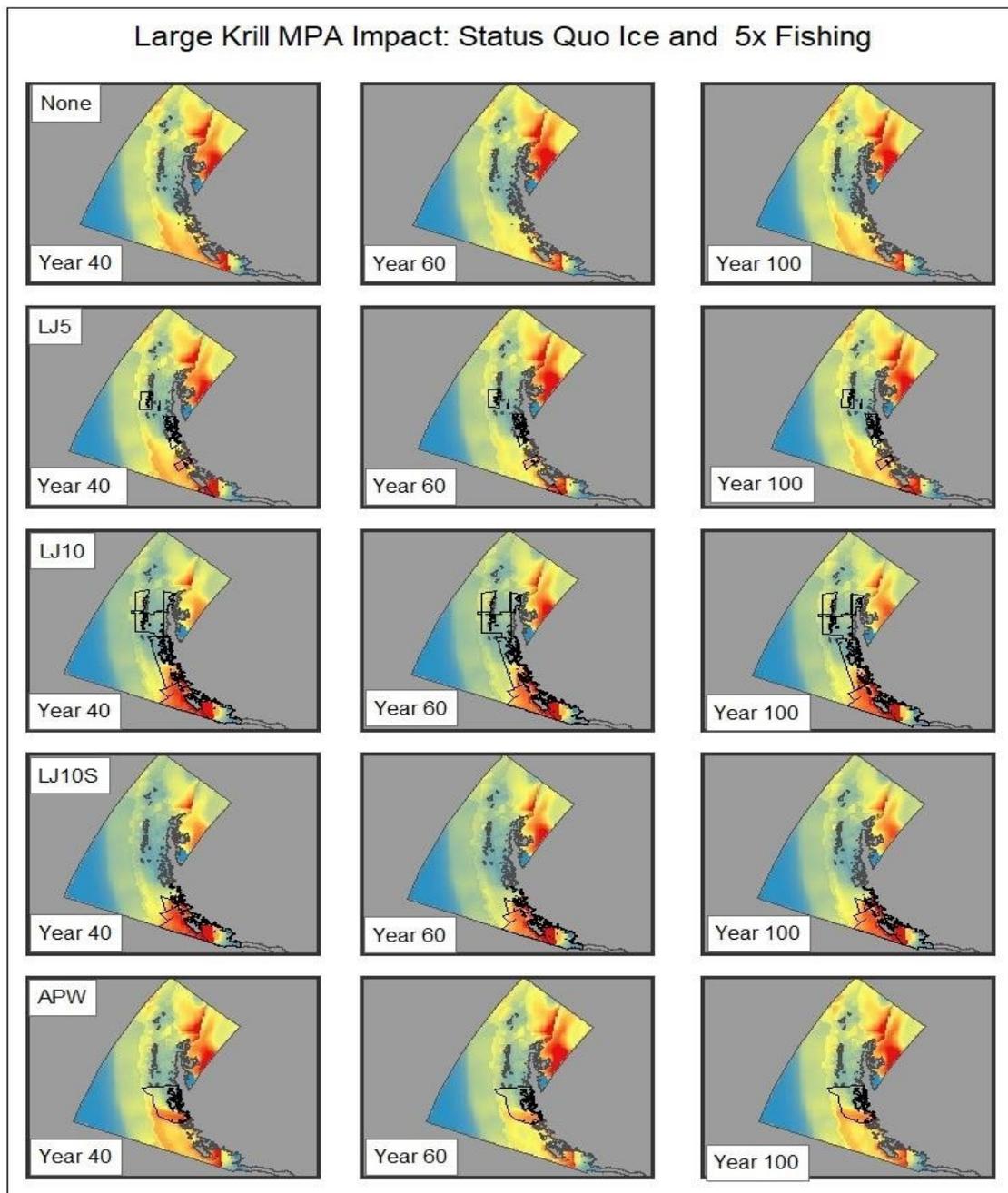


Appendix 7 xxviii *N. rossii* in Status Quo Ice Scenario under 5x Fishing Pressure. Red color indicates areas of greater concentration.

Large Krill MPA Impact: Status Quo Ice and Status Quo Fishing

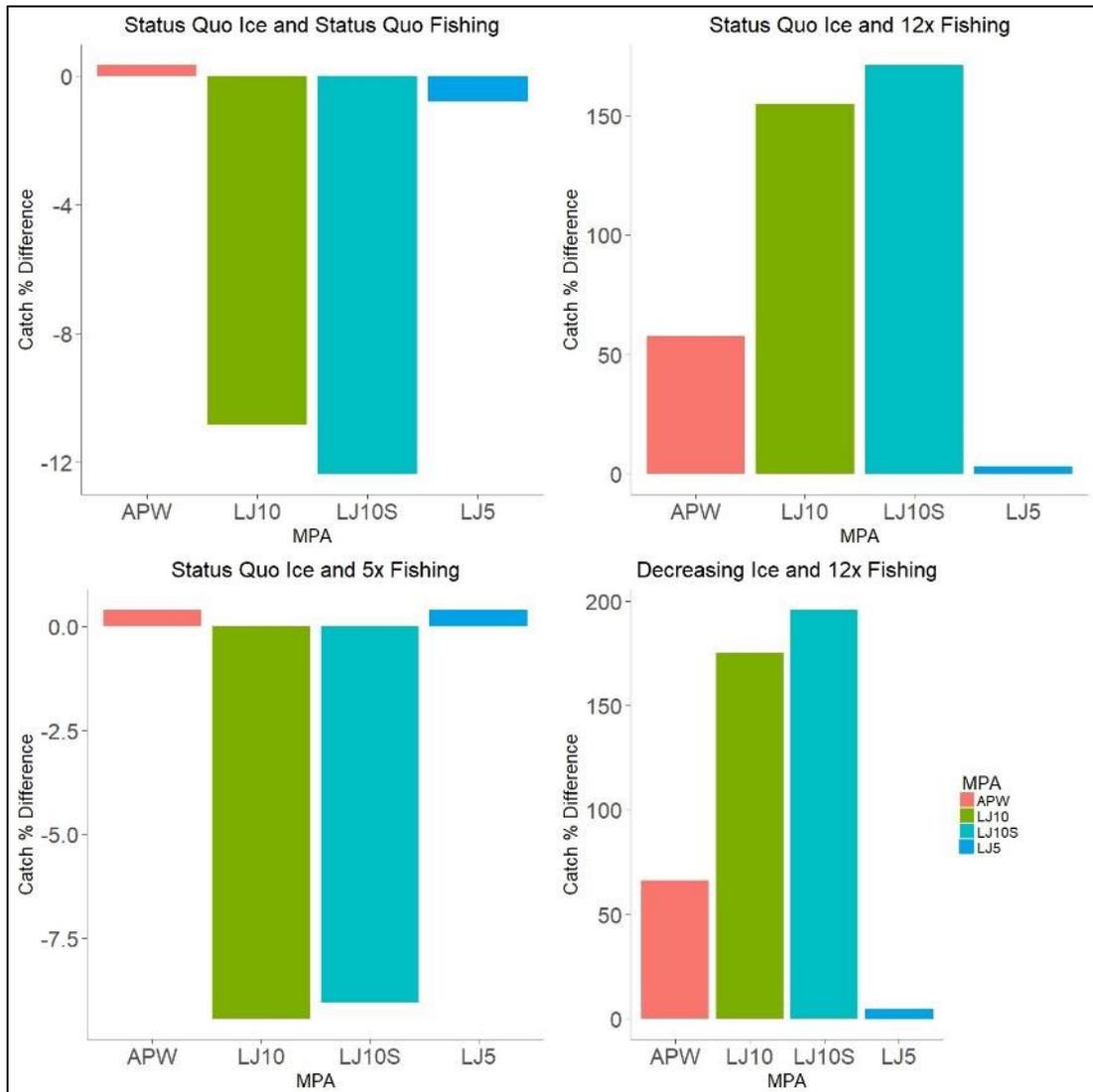


Appendix 7 xxix Krill in Status Quo Ice Scenario under Status Quo Fishing Pressure. Red color indicates areas of greater concentration.



Appendix 7 xxx Krill in Status Quo Ice Scenario under 5x Pressure. Red color indicates areas of greater concentration.

Appendix 8 Catch comparisons



Simulated catches differences compared to the no MPA scenario. The presence of any MPA improved catches, while the biggest gains were realized by the LJ10 and LJ10S scenarios. Simulated catches under 12x fishing level saw a positive impact from all MPA scenarios.

BIOGRAPHY

Adrian Dahood-Fritz graduated from Choate Rosemary Hall High School, Wallingford, Connecticut, in 1997. She received a Bachelor of Science (Zoology) and second Bachelor of Science in Fisheries from the University of Washington in 2001. She was employed as a field ecologist in various projects around the world for three years before earning her Masters of Science at Texas A&M University in 2009. She was then employed as the Environmental Policy Specialist in the Office of Polar Programs at the National Science Foundation for four years. With encouragement