

Effects of Harvest and Climate Change on Polar Marine Ecosystems

Case Studies from the Antarctic Peninsula and Hudson
Bay

by

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Abstract

This thesis applies food web modelling to increase our understanding of how the interaction of climate change and exploitation have historically altered, and continue to alter, marine polar ecosystems. Understanding stressors responsible for ecosystem level changes is important not only to the people and industries reliant on the resources, but for managers to make future decisions on resource uses. The first two chapters develop models of Hudson Bay (Arctic) and Antarctic Peninsula (Antarctic) marine ecosystems, focused on re-creating changes in the past 30 years. Both ecosystems have undergone changes due to environmental factors, which are incorporated into the models. While the Hudson Bay model exhibits a shift from benthic to pelagic species, the Antarctic Peninsula model is identified to have more uniform declines across all species, as the main trophic link in the ecosystem, Antarctic krill declines. Model simulations are continued in the next two chapters, whereby future environmental changes are tested in conjunction with multiple exploitation levels. For Hudson Bay, continued harvest of marine mammals at current conditions results in large-scale declines for some species (narwhal, eastern Hudson Bay beluga, polar bears, and walrus), indicating current harvest levels are too high to sustain long term. Further shifts from benthic to pelagic species in the lower trophic levels favor fish species such as capelin and sandlance. Future simulations of the Antarctic Peninsula identify large reductions in ecosystem biomass of all species due changes in environmental conditions and an overall reduction in krill, with minimal ecosystem impacts from harvest. In the last chapter, an economic model is constructed to assess the use value of hunting narwhal and beluga in the Hudson Bay region. The economic impact to northern residents is considered as future model simulations of Hudson Bay reveal that these species may be susceptible to population declines, and issues of food security are becoming increasingly important. Economic analysis reveals the motivation to hunt in Hudson Bay may not be economically-driven, there are substantial benefits derived by northern communities through narwhal and beluga hunts. Results for each ecosystem are discussed as they pertain to future research and management of each ecosystem.

Preface

A version of chapter 2, co-authored with Tony Pitcher and Villy Christensen, has been re-submitted with revisions to Ecological Modelling. I constructed the model and wrote the manuscript. Villy Christensen was key in the development of the model structure, fitting of the model, and other technical model aspects. Tony Pitcher provided guidance on model construction and discussions on the direction of the manuscript.

A version of chapter 4, co-authored with Tony Pitcher and Villy Christensen, has been re-submitted with revisions to Ecological Modelling. I created the model simulations and wrote the manuscript. In addition to their assistance with chapter 2 which utilizes the same model, both Villy Christensen and Tony Pitcher provided guidance with the future simulations. Villy Christensen also provided technical model assistance.

A version of chapter 6, co-authored with Megan Bailey, Jeff Higdon, Steve Ferguson, and Rashid Sumaila, has been re-submitted with revisions to the journal Arctic. I conceptualized and constructed the model in addition to writing the manuscript. Megan Bailey assisted in model construction. Rashid Sumaila and Megan Bailey provided the framework for the model and assistance on economic analyses. Jeff Higdon and Steve Ferguson provided expertise on model parameters, in addition to Jeff Higdon collecting input parameter values during fieldwork in the north. All authors provided feedback on the submitted manuscript.

Chapters 3 and 5 are co-authored with Tony Pitcher and Evgeny Pakhomov, and will be submitted to a peer-review journal. I constructed the model for chapter 3, created the model simulations for chapter 5, and wrote both manuscripts. Tony Pitcher provided the idea for the model and guidance throughout the model construction, and provided guidance with model simulations. Evgeny Pakhomov was key in providing expertise to the ecology of the model which was important to the fitting process, and contributed to the ecological relevance of the model.

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Dedication

To William, Diane, and Travis.

Chapter 1

Introduction

The main aim of this thesis is to address the impacts of harvest and environmental changes on two polar ecosystems; one Arctic and one Antarctic. Both regions aim to manage with an ecosystem-based approach (CCAMLR, 1980; Anonymous, 2006), implying that exploitation of target species should not cause destruction of other species. For both ecosystems, the following questions formed the chapters presented in the thesis. (1) What did the past ecosystem look like? (2) What factors caused past changes in the ecosystem? (3) How will these factors continue to impact the ecosystem in the future? And lastly, (4) For the Arctic ecosystem where people rely on harvest for subsistence, how might these changes affect these communities?

This first chapter aims to provide a background into both of the case study areas. First, I provide information on the geographic regions, and the environmental factors that shape them. Second, I address the management of each area, and the goals of the managers within the context of the ecosystem. Last, this chapter provides a summary of the questions and research completed in each chapter of the thesis.

1.1 Ecosystem-Based Management

The focus of this thesis is on two polar ecosystems with the intent to identify prominent stressors that have, or will in the future, alter ecosystem structure. The overall goal is to provide this information so that future research and management decisions can take into account the ecosystem dynamics of environmental change and exploitation. Fisheries regulation within the context of an entire ecosystem has become more prominent in recent years with the development of management strategies such as 'Ecosystem-Based

Management' (EBM), 'Ecosystem-Based Fisheries Management' (EBFM), and 'Ecosystem Approach to Fisheries' (EAF). Despite the different terminologies, these management strategies share many of the same goals such as maintaining natural structure and function of the ecosystem, preventing declines of target and non-target species, and identifying environmentally sustainable development of resources (Ward et al., 2002; Hall and Mainprize, 2004; Pitkitch et al., 2004; Scandol et al., 2005).

It has been noted that management priorities should be focused on the ecosystem as a whole, rather than just target species (Pitkitch et al., 2004). Yet as these phrases have only in recent years begun appearing in the literature and management plans, the foundations of EBM are deep-rooted within many international agreements. The United Nations Convention on the Law of the Sea, an international agreement between 162 countries, notes harvest of species should be accomplished while maintaining or restoring populations of harvested and dependent species for both coastal and high seas fisheries (United Nations, 1982, articles 61 and 191). The same year the Commission for the Conservation of Antarctic Marine Living Resources came into effect regarding the management of the Antarctic. Article II of the convention specifically addresses harvest in that it should prevent irreversible changes in the ecosystem and maintain ecological relationships between harvested, dependent, and related populations (CCAMLR, 1980; Constable et al., 2000). In 1992, the Rio Declaration on the Environment and Development called for the use of the precautionary principle in order to protect the environment (United Nations, 1992, principle 15). Individual countries such as the US, Canada and Australia have also integrated aspects of EBM into their management plans for specific areas or fisheries (Quinn and Theberge, 2004; Scandol et al., 2005; Pace, 2009).

Evaluation of aquatic ecosystems through models such as EwE (Ecopath with Ecosim) and Atlantis allow for fisheries assessments at the ecosystem level (Scandol et al., 2005), and the first four chapters of this thesis address this. In addition to ecological aspects of EBM, social and economic goals are also considered for the success of EBM (Hilborn et al., 2004). Scandol et al. (2005) noted the importance of management to recognize that in addition to

harvesting, there are additional uses and values of the ecosystem that must be considered. As human values drive the management process, and the human uses and values are an important component to EBM, these must be considered for management to be successful (Ward et al., 2002). It is for these reasons that I have included a chapter estimating the economic use value of hunts in Hudson Bay.

1.2 Study Areas

Two regions were chosen as case studies for the thesis; one from the Arctic and one from the Antarctic. From the Arctic, Hudson Bay was chosen. Although Hudson Bay is considered sub-Arctic in location, its weather patterns are reflective of a higher latitude region, with many high Arctic species residing there such as polar bears (Stirling and Parkinson, 2006). In addition, collaboration with researchers at the Department of Fisheries and Oceans Canada (DFO) Central and Arctic Division in Winnipeg, Manitoba as part of their International Polar Year (IPY) Global Warming and Arctic Marine Mammal (GWAMM) project dictated the study area. For the Antarctic case study, the Antarctic Peninsula was selected. It is considered one of the fastest warming areas in the world (Anisimov et al., 2001; Hansen et al., 2006a), while other areas of the Antarctic have shown to be in a cooling trend (Turner et al., 2005). The central species in this ecosystem, krill (*Euphausia superba*), have shown declines linked to environmental changes in addition to being directly harvested (Atkinson et al., 2004; CCAMLR, 2008b).

Hudson Bay

Physical Environment

Hudson Bay is a large, shallow, low nutrient marine area which freezes and thaws annually (Markham, 1986; Stewart and Lockhart, 2005; Stewart and Barber, 2010). Ice and temperature within this region are more reflective of a high Arctic ecosystem, allowing species normally found at higher latitudes to be found within Hudson Bay (Maxwell, 1986; Stewart and Barber,

1.2. Study Areas

2010). The Hudson Bay watershed is the second largest in Canada, capturing roughly 30% of all Canadian runoff (Natural Resources Canada, 1999). The timing of freshwater and nutrients inputs can have large impacts on the type and amount of annual primary production (Stewart and Barber, 2010). Seawater enters and exits via Hudson Strait, and circulates in a counter-clockwise direction (Stewart and Lockhart, 2005). The cooler deeper waters characteristic of Hudson Strait potentially act as a thermal barrier, preventing species from entering Hudson Bay. This divide is believed to be a choke-point for migratory species, such as killer whales, and it is believed that this divide will open as climate warms (Higdon and Ferguson, 2009). Being classified as a polar ecosystem, ice is an important component in the life cycle of many organisms, ranging from algae frozen within the sea ice (Horner et al., 1992), to top predators such as polar bears who use ice as a foraging platform (Stirling et al., 2004). Increases in temperature combined with lengthening of the ice-free season have increased concern for species residing in Hudson Bay (Parkinson et al., 1999; Gagnon and Gough, 2005; Hansen et al., 2006b).

Resource Uses

Hudson Bay has been used for roughly 4000 years by nomadic hunters who depended on marine mammals, fish and land animals such as caribou for subsistence (Stewart and Lockhart, 2005). European activity in the region started in the 17th century, as explorers searched for the northwest passage. Henry Hudson (Hudson Bay's namesake) was the first recorded explorer into Hudson and James Bays (Francis and Morantz, 1983). Continued expeditions into the region and the abundance of available furs, primarily beaver, led to the establishment of the Hudson's Bay Company (Stewart and Lockhart, 2005). Harvest of fur-bearing animals by natives increased to meet the supply demands of the Europeans, although this conflicted with ancient spiritual beliefs (Sokolow, 2003). While other animals were also harvested for fur, beavers were specifically targeted, with their pelts used as currency between Europeans and Aborigines before populations crashed

1.2. Study Areas

(Homren, 2004). As the fur trade declined, interest in whaling became more prominent (Francis and Morantz, 1983). Prior to the commercial whaling of bowhead whales, Hudson's Bay Company had small-scale unsuccessful attempts at commercial whaling operations for belugas (Reeves and Mitchell, 1987). The Northwest Company, a fur trading company formed in Montreal which later merged with the Hudson's Bay Company, and the Hudson's Bay Company operated posts in Hudson and James Bays related to whaling and trade (see Stewart and Lockhart, 2005, table 11-3 for a full list of settlements). American and Canadian vessels commercially harvested bowhead whales from 1860 to 1915, causing a large population decline before commercial whaling commenced in the region (Ross, 1974).

Presently, subsistence harvest is allowed for many species with varying levels of regulation. Narwhal, beluga and polar bears have quotas and are harvested annually, while bowhead whales are considered endangered and are rarely harvested (DFO, 1998; Cosens and Innes, 2000; Hammill, 2001; Lunn et al., 2002). Seals, walrus, birds, fish and invertebrates are harvested by Aborigines (Inuit and Cree) without a license and can be taken throughout the year (Berkes, 1977; Wein et al., 1996; Stewart and Lockhart, 2005). A license is required for sport hunters to harvest birds within the area (Stewart and Lockhart, 2005). The only commercial fishing operation is for Arctic char along the river mouths, but this fishery yields small catches (Carder and Peet, 1983; DFO, 1997). Presently, most communities surrounding Hudson Bay are inhabited by first nations, making up 85% of the total population in Nunavut, most of which are Inuit (Statistics Canada, 2006).

Management

The territory encompassing Hudson Bay is divided between the provinces of Manitoba, Ontario and Quebec, and the Nunavut territory. Within Quebec, indigenous people (Inuit and Cree) live in Nunavik, the name for the northern third of the province. The first major agreement between Quebec and the Inuit was the James Bay and Northern Quebec Agreement in 1978 to give environmental and social protection (Anonymous, 1975).

1.2. Study Areas

The territory of Nunavut was established in 1999, separating it from the pre-existing Northwest Territories. Management for the Ontario and Manitoba portions of Hudson Bay is regulated by DFO, while the Nunavut portion is governed by the Nunavut Wildlife Management Board (NWMB). The Nunavut Land Claims Agreement, signed into effect in 1993, gives management authority of wildlife within Nunavut to the NWMB (Nunavut Land Claims Agreement, 1993). The NWMB consists of appointed members which are responsible for establishing, modifying, or removing levels of total allowable harvest. In 2006, the Nunavik Inuit Land Claims Agreement established the Nunavik Marine Region Wildlife Board (NMRWB) and granted Nunavik Inuit the right to harvest wildlife species to fulfil their economic, social, and cultural needs (Anonymous, 2006).

From 1996-2001 the NWMB conducted the Nunavut Wildlife Harvest Study to collect data for species within Hudson Bay for which it was responsible (Nunavut Wildlife Management Board, 2000). This harvest study was to help provide baseline information for all of Nunavut, for which to base total allowable harvests, primarily for marine mammal species (Priest and Usher, 2004). The total allowable harvest must be approved by the NWMB, and they retain the right to alter harvest levels in the future. The Nunavik parallel to this board, NMRWB, is responsible for the harvesting of species within the Nunavik and James Bay portions of Hudson Bay regarding Inuit harvest. The Canadian government, specifically DFO, can disallow decisions set by the NWMB for reasons of conservation, public safety, or public health (Nunavut Land Claims Agreement, 1993). The federal government also holds the power to interfere regarding harvest in Nunavik.

Antarctic Peninsula

Physical Environment

The Southern Ocean surrounds Antarctica, and while there are no physical barriers separating this ocean from the surrounding waters, the Antarctic Polar Front (or Antarctic convergence) is where the colder Antarctic waters sink below the warmer sub-Antarctic waters forming a thermal barrier

1.2. Study Areas

between 50°S to 60°S (Knox, 1994). Two main current systems occur in the Antarctic. The first is the Antarctic Circumpolar Current (ACC) or west wind drift, which flows east around the continent, near the Antarctic Convergence and carries with it nutrient rich upper circumpolar deep water (Tynan, 1998; Fallon and Stratford, 2003). The second is the coastal current (east wind drift) which moves towards the west as a counter current to the ACC. It moves close to the continent, and is responsible for forming eddies close to the shelf (Knox, 1994).

The Antarctic Peninsula is the only land mass to extend from the continent. Along with the tip of South America, this peninsula impedes both wind and ocean currents in the Southern Ocean through Drake Passage, the area between the two peninsula tips (Fallon and Stratford, 2003). The ACC moves faster through this area and constricts to bring in warmer water originating from the Bellingshausen Sea (to the west) towards the Scotia Sea (to the east) (Hewitt et al., 2002). The constriction of the ACC in this area forces the southern boundary (southern limits of the ACC) close to the continent at the Antarctic Peninsula (Tynan, 1998). In addition to the southern boundary, wind and bathymetry also contribute to the high productivity of the area and the large biomass of Antarctic krill (*Euphausia superba*) (Prezelin et al., 2000).

Seasonal ice conditions are also a feature of the region, with the extent of sea ice as an important factor for many ice-associated species. Observed declines in sea ice and increases in temperature are more extreme at the Antarctic Peninsula than other Antarctic locations (Doake and Vaughan, 1991; Anisimov et al., 2001; Cook et al., 2005; Hansen et al., 2006a). One of the most studied species in the Antarctic, krill, has been identified to be a key link in the Antarctic food web, in addition to having stages of its life history associated with sea ice (Marschall, 1988; Daly, 1990; Moline et al., 2000). Future changes to the environment are expected to impact krill, and subsequently, the rest of the food web.

Resource Uses

Resource use in the Antarctic began with the discovery of seals at South Georgia before moving on to whaling, fishing, and finally krill harvest. Sealing in the Antarctic began after Captain Cook reported large populations of fur seals in the sub-Antarctic islands (Kriwoken and Williamson, 1993). Seals were targeted for their pelts, with Antarctic and sub-Antarctic fur seals making up the majority of catches in the late 1700s to early 1800s with over 1.2 million harvested by 1822 (Agnew et al., 2000). While fur seals were the early targets of sealing fleets, elephant, Ross, crabeater, and Weddell seals have all been targeted, with many populations being largely reduced by harvest (Fallon and Stratford, 2003). The Convention on the Conservation of Antarctic Seals (CCAS) was established in the 1970s to set catch limits for seals, and prevents the commercial harvest of seals south of 60°S (Agnew et al., 2000).

During the era of seal harvest, penguins were also harvested, primarily for oil (Agnew et al., 2000). Whaling began as seal resources declined. Commercial whaling in the Antarctic was initiated in 1892 and continued until 1982, when the International Whaling Commission (IWC) issued a moratorium on whaling (Fallon and Stratford, 2003; International Whaling Commission, 2009). Whaling started at South Georgia before expanding to other sub-Antarctic islands and further south to the continent (Agnew et al., 2000). Humpback, minke, blue, sei, southern right and sperm whales have all been harvested in the Southern Ocean (Fallon and Stratford, 2003). Due to large declines in many whale populations, the IWC assigned humpback and blue whales protected status in 1963 and 1964, respectively (Kriwoken and Williamson, 1993). The Southern Ocean was declared a whale sanctuary in 1994 by the International Whaling Commission prohibiting ship or land-based whaling operations (Agnew et al., 2000). Japan objects to the moratorium and continues to harvest whales, claiming scientific whaling, with their primary target being minke whales in the Southern ocean (Agnew et al., 2000).

A fishery for finfish species; mackerel icefish (*Champscephalus gunnari*),

1.2. Study Areas

spiny icefish (*Chaenodraco wilsoni*), marbled rockcod (*Notothenia rossi*), humped rockcod (*Notothenia gibberifrons*), blackfin icefish (*Chaenocephalus aceratus*), and ocellated icefish (*Chionodraco rastrospinosus*) was open from 1978 to 1989 in the Antarctic Peninsula area (Kock, 1998). Since the fishery closure there is currently some exploratory fishing, but no re-opening of finfish fishing. Patagonian and Antarctic toothfish (*Dissostichus eleginoides* and *Dissostichus mawsoni*) were harvested within the Southern Ocean starting in the mid 1980s (Agnew et al., 2000). The majority of catches from this fishery are taken from South Georgia, with limited catches recorded for only a few years within the Antarctic Peninsula area (CCAMLR, 2008b).

Following a decade of exploratory fishing Antarctic krill, became a target species when the commercial fishery opened in 1972 (Nicol and Endo, 1999; Agnew et al., 2000). Japan, the Soviet Union, and Russia obtain the majority of krill catches, with large numbers harvested from the Antarctic Peninsula (Nicol and Endo, 1999; CCAMLR, 2008b). The fishery operates year-round with catches closer to the continent occurring primarily in the austral summer, and catches from sub-Antarctic areas (South Georgia) in winter months (Nicol and Endo, 1999). Observed declines in krill stocks over the last 20 years are associated with changes in environmental conditions (Atkinson et al., 2004). While the quota for krill is much higher than annual catches, in 2010 catch biomass increased to nearly double the values from 1994-2009 (Nicol et al., 2012).

Management

The Antarctic Treaty, which entered into force in 1961, established freedom of scientific information in the Antarctic in addition to establishing its use for peaceful purposes (Anonymous, 1959). Prior to this, the International Whaling Commission was responsible for managing species in the Southern Ocean (Fallon and Stratford, 2003). In 1982 the Commission on the Conservation of Antarctic Marine Living Resources (CCAMLR) was established (CCAMLR, 1980). It has been considered one of the first regulating agencies to establish an ecosystem approach to managing resources (Constable

et al., 2000).

In 1985 CCAMLR established the Ecosystem Monitoring Program (CEMP) in order to regulate harvest in accordance with the ecosystem approach. CEMP monitors both harvested and dependent species to estimate predator, prey and environmental performance parameters around the Antarctic (Agnew, 1997). The monitoring program assists CCAMLR in parameterizing models for use in establishing quotas.

1.3 Ecopath with Ecosim

The majority of this thesis applies the Ecopath with Ecosim (EwE) approach to construct ecosystem models and simulate changes over time. The Ewe approach originated with a single mass-balanced Ecopath model based in Hawaii (Polovina, 1984), and has expanded throughout development to include numerous additional features for assessing ecosystems. Temporal simulations (Ecosim) and spatial analysis abilities (Ecospace) were later added to aid in assessments of fishing policies and formation of protected areas (Walters et al., 1997, 1999, 2000). Indices to explore the health of the ecosystem were developed through a series of network analyses (Christensen and Pauly, 1992; Christensen, 1995). Additional features such as automated mass-balance with incorporation of Monte Carlo for better parameter estimation and network analysis have been added throughout development (Kavanagh et al., 2004). EwE is used in over 154 countries, with over 300 papers published, and has been named one of NOAA’s top 10 breakthroughs (NOAA, 2006). An updated version is now in use to allow greater flexibility in user programming and coupling between other modelling programs (Christensen et al., 2007; Buszowski et al., 2009).

Ecosystem models, specifically EwE, have been developed to evaluate ecosystem effects of fishing and environmental change (Christensen and Walters, 2004), which are the main objectives of the thesis. Single species models may prove efficient when assessing one species, but they are unable to identify potential impacts caused by linkages within the ecosystem (Fulton and Smith, 2004). Multispecies models are able to identify non-intuitive changes

1.4. Thesis Outline

in biomass through species interactions within the model, and may assist in evaluating ecosystem impacts of management policies (Walters et al., 1997; Fulton and Smith, 2004).

While other modeling tools exist (see Plaganyi, 2007, for a detailed comparison of ecosystem modelling tools), EwE was selected over single species models due to ease of use and scope of the thesis. Ecosystem modelling tools such as Atlantis are considered to be the most complete when assessing entire ecosystems as it represents both biological and physical interactions within an ecosystem, however large amounts of data are required in addition to sub-models to address bio-geochemical interactions (Fulton and Smith, 2004; Plaganyi, 2007), which are beyond the scope of the thesis. Limitations to ecosystem and other multi-species approaches to modelling are rooted in the quality and availability of data (Plaganyi and Butterworth, 2004). The EwE approach allows users an existing model framework in addition to the ability of the software to focus on fishery and environmental issues (Christensen and Walters, 2004; Plaganyi and Butterworth, 2004). As models should aim for the 'minimum realistic' approach to avoid over-parameterization (Fulton et al., 2003), the EwE software was selected as the most capable tool for the thesis.

1.4 Thesis Outline

Managers are becoming increasingly focused on policies that include an ecosystem-based management approach, meaning the context of the ecosystem is considered when policies are focused around a particular species. Ecosystem models can identify potential impacts that a series of single-species models cannot (Fulton and Smith, 2004). Furthermore, management policies focusing on single species have the potential to overlook important indirect trophic linkages to targeted species. Within this thesis, I investigate the impacts of harvest on all species in the ecosystem within the same time scale in conjunction with known or theorized impacts from environmental changes. The goal of this thesis is to identify important stressors to each ecosystem, and how future changes in these stressors may impact ecosystem

structure.

Chapters 2 and 3

Chapters 2 and 3 use the Ecopath with Ecosim software (Walters et al., 1997; Christensen et al., 2005) to assess past changes in ecosystem structure for Hudson Bay and the Antarctic Peninsula respectively. Models were constructed based on past ecosystem structure and projected forward to the present day focusing on catch and environmental changes that have occurred. Methods for using Ecosim simulations to recreate past catch and environmental trends is well established, and has been explored for a multitude of ecosystems, including the Gulf of Alaska and Aleutian Islands, northern British Columbia, Raja Ampat Indonesia and the northern Ionian Sea (Guenette et al., 2006; Ainsworth et al., 2008b,a; Piroddi et al., 2010).

In chapter 2, data from all species are combined to assess the trophic structure of the Hudson Bay food web through diet linkages. As part of the IPY project on marine mammals, this chapter explores the potential causes of changes to marine mammals and the rest of the ecosystem with respect to climate change. Declines in some stocks of marine mammals (polar bears, eastern Hudson Bay beluga and narwhal), have prompted research on the reasons for these changes, in part to determine if climate change has had an impact (Stirling et al., 1999; COSEWIC, 2004a; Stirling et al., 2004; Hammill et al., 2009). I first identified the ecosystem structure through literature reviews and assistance from researchers at the Department of Fisheries and Oceans Central and Arctic Division in Winnipeg, Canada. I was able to assess gaps in data, such as the biomass of fish groups, through modeling approaches, such as the Monte Carlo routine in EwE (Christensen and Walters, 2004). After the initial structure of the model was complete, re-creation of past trends in Ecosim were performed. Catch records for marine mammal species were readily available from government records, but information on other species was lacking. Changes in the diets of thick-billed murres indicated shifts in the fish community from benthic to pelagic species (Gaston et al., 2003). This was coupled with information on lower trophic levels

from other Arctic ecosystems to gain an understanding of past changes to the ecosystem.

In chapter 3, the past Antarctic Peninsula ecosystem was recreated in the same manner as the Hudson Bay ecosystem (chapter 2). Previous assessments of the Antarctic Peninsula have utilized the EwE methods (Efran and Pitcher, 2005; Cornejo-Donoso and Antezana, 2008), however, they have not included environmental factors. This chapter expands on past research to incorporate different environmental variables to explain declines in krill biomass, and increases in salp groups (a gelatinous tunicate and perceived competitor of krill) in conjunction with harvesting trends. This chapter tests the likelihood of different environmental variables as causing the changes in salp and krill abundance based on ecological studies (Marschall, 1988; Loeb et al., 1997; Brierley and Watkins, 2000; Atkinson et al., 2004; Lee et al., 2010; Flores et al., 2011). I also explore the effects of increasing the harvest of krill to quota levels. As the krill fishery operates on what is considered a keystone species (Quetin and Ross, 1991; Moline et al., 2004), annual catches are only roughly 10% of the quota limits (Hewitt et al., 2002, 2004). This chapter explores the potential repercussions of harvesting krill at full quota levels.

Chapters 4 and 5

Chapters 4 and 5 build on chapters 2 and 3 respectively, by extending simulations into the future. Ecosim scenarios are routinely used to explore fishing strategies in future scenarios (Araujo et al., 2008; Heymans et al., 2009) particularly in an economic context. However, rather than focusing on maximizing profits or other policy objectives, these chapters explore future ecosystem states and address the ecological structure rather than policy objectives. Each chapter utilizes different levels of harvest and environmental drivers previously identified to assess potential future states of each ecosystem. Data from global climate models GFDL (2010) allowed for environmental drivers to be continued into the future in conjunction with IPCC (Intergovernmental Panel on Climate Change) scenarios. Catch scenarios for

each ecosystem are based on either current harvest levels or are increased to simulate higher quotas in the future. These chapters identify species within each ecosystem likely to be impacted by harvest or environmental changes in the future.

Chapter 6

Chapter 6 focuses on the human component to the Hudson Bay ecosystem by providing an economic assessment to the harvest of narwhal and beluga. Many species are currently harvested within Hudson Bay by Inuit, however cetacean species have been a prominent focus of the Inuit diet for thousands of years (Stewart and Lockhart, 2004; Freeman, 2005). Narwhal and beluga were selected as the focus for an economic assessment of hunting. Model simulations from chapters 2 and 4 identify declines in narwhal and the eastern Hudson Bay beluga indicating their potential lack of availability in the future. Focussing on these two hunts, the economic use value is explored primarily through the costs and revenues associated with harvesting narwhal and beluga. Past economic assessments in the north have been limited and focused on one or more aspects of individual hunts rather than an overview (Weaver and Walker, 1988; Reeves, 1992a). Previous studies have assessed the economic value of hunting in specific high Arctic communities Loring (1996), however this has not been attempted for the Hudson Bay region. This chapter provides a summary of economic components associated with the harvesting of these two species. In addition to providing an estimate on the total economic use value for each of these hunt, costs and revenues are also assessed based on each community participating in the harvest.

Chapter 7

Chapter 7 provides a summary and discusses the results of the thesis in the context of managing ecosystem. Directions for future research and applications to management are presented.

Chapter 2

Impacts of Hunting, Fishing, and Climate Change to the Hudson Bay Marine Ecosystem 1970-2009

2.1 Synopsis

An ecosystem model was created for the Hudson Bay region, Canada, for 1970-2010, aiming to identify ecosystem linkages while bringing together research from diverse research sources. The research presented was completed as part of the International Polar Year Global Warming and Arctic Marine Mammal project, focusing on the impacts of climate change on marine mammals. The model presented in detail here synthesizes research spanning all trophic levels for incorporation into the Ecopath with Ecosim (EwE) modeling framework. The Ecopath model, containing 40 functional groups, identifies a previously unestimated fish biomass of $3.42t \cdot km^{-2}$ for the region, based on the trophic linkages and diets within the food web. Catch and abundance data for the Hudson Bay region, along with environmental drivers (sea surface temperature and ice cover) were used to re-create past changes to the ecosystem through the fitting of individual groups. The Ecosim model captures many dynamics present in the system, while identifying gaps in existing data for future research and as the basis for work simulating climate change and its impacts on the ecosystem. A general shift in lower trophic levels from a sea ice to benthos to benthic fish pathway to

one favoring pelagic phytoplankton to zooplankton to pelagic fish. Declines in polar bear, narwhal, and eastern Hudson Bay beluga model groups identifies harvest as the main stressor. Simulations testing the model sensitivity to hunting and environmental pressures indicate the biomasses of higher trophic level organisms (marine mammals) are more responsive to hunting pressures while lower trophic levels (benthos, zooplankton) are more easily influenced by climate drivers.

2.2 Introduction

Polar regions are increasing in temperature faster than temperate areas, with Arctic temperature rising at almost twice the rate of the rest of the world (ACIA, 2004). The fourth International Polar Year (IPY) in 2007-2009 highlighted the need for research to increase our knowledge of the dynamics occurring in Polar areas.

While Hudson Bay (HB) (figure 2.1) is geographically considered sub-Arctic, between 50-70°N, this system reflects high Arctic attributes such as climate, biogeography, and higher trophic level animals. For example, polar bears, are found at their lowest latitudinal range in HB, due to the cold winters and the ice available for foraging (Stirling and Parkinson, 2006). Moreover, many species present in this ecosystem have adapted to the seasonal ice cycle, from whales occupying the region during the ice free seasons, and seals breeding on the ice, to the ability of smaller zooplankton to survive winter months using nutrients frozen within the sea ice (Poltermann, 2001; Stewart and Lockhart, 2005).

Research in HB has been limited in the past, compared to other Arctic ecosystems. Two surveys of phytoplankton and zooplankton have been completed in HB assessing lower trophic levels; one in 1993 sampling from James Bay (JB) along the east coast of HB into Hudson Strait (HS) (Harvey et al., 1997, 2001), and a second in 2003 running east to west through the middle of HB (Harvey et al., 2006). The most comprehensive benthic summary from numerous locations in HB from 1953 to 1956 (Atkinsor and Wacasey,

2.2. Introduction

1989) recorded only the presence of benthic species. Fish are poorly understood, although there is the general belief that fish are not abundant in HB, a situation somewhat verified by unsuccessful commercial fishery ventures in the past (Stewart and Lockhart, 2005). Marine mammals are some of the most well studied species in the region, although only a handful of surveys have been completed for each species (Ferguson et al., 2010).

Surface temperatures in HB have increased by 0.5-1.5°C during 1955-2005 (Hansen et al., 2006a), and sea ice extent decreased by $2000 \pm 900 \text{ km}^{-2} \text{ y}^{-1}$ between 1978 and 1996 (Parkinson et al., 1999). These changes combined with a longer ice free season (Gough et al., 2004; Gagnon and Gough, 2005) are likely yielding large scale changes to the sympagic marine ecosystem. Ice algae, which contributes up to 57% of primary production in some Arctic regions (Gosselin et al., 1997), and roughly 25% of total production in some areas of Hudson Bay (Legendre et al., 1996), can be stored through the winter within the sea ice. Therefore, the loss of sea ice will alter the availability of algae stored within the sea ice, which will cause shifts in the ecosystem by altering energy transfer to higher trophic levels. Such shifts have already been observed in bird diets as indicated by declines in Arctic cod (*Boreogadus saida*) and benthic fish species such as sculpins (Family: Cottidae) and zoarcids (Family: Zoarcidae) with increases in pelagic fish such as capelin (*Mallotus villosus*) and sandlance (*Ammodytes spp.*). Polar bear populations are at their southern limit in HB, and already experience longer summers than their northern counterparts. Lengthening of the ice free summer is believed to increase nutritional stress as there is less ice to forage on, decreasing their hunting platform, and making polar bears vulnerable to sea ice declines (Stirling and Derocher, 1993; Stirling et al., 1999).

Along with environmental changes, human uses of the ecosystem also have the potential to alter the abundance of species. Currently all marine mammal species are hunted annually, with the exception of bowhead where harvest only occurs in specific years. Quotas are imposed on the harvest of certain cetacean species. Seabirds and fish are also harvested, however these are generally unregulated. Since the 1970, human populations

have nearly tripled (Bell, 2002; Statistics Canada, 2006; Nunavut Bureau of Statistics, 2008; Sutherland et al., 2010) with increases in harvest levels for many species also being recorded. Understanding whether these stocks can withstand the continuous pressure of harvest is important, and even more so in conjunction with the impacts of climate change. In order to test the importance of multiple stressors on the ecosystem, we have constructed an ecosystem model to re-create the dynamics from 1970-2009.

The ecosystem model was created using the Ecopath with Ecosim software (Buszowski et al., 2009; Christensen et al., 2007), to assess the Hudson Bay ecosystem with a mass-balance model. Through the construction of an Ecopath model, gaps in existing ecosystem knowledge can be identified. For example, biomass of fish populations are obtained by assessing the demands of predators and the amount of fish which can be supported by lower trophic levels, based on food web structure. Ecosim temporal simulations (Walters et al., 1997; Christensen and Walters, 2004) are used to re-create observed changes since 1970, helping to identify causes to changes in ecosystem structure. The model aims to focus on the impact of climate change and hunting on marine mammal species as part of the Global Warming and Arctic Marine Mammal International Polar Year research project, therefore giving marine mammals a greater presence in the model structure. While high and low trophic level organisms are relatively well studied in this region, serious gaps regarding mid trophic level organisms (primarily benthos and fish) exist. Despite these gaps, there is an urgency to understand a system that is subjected to multiple stressors. This modeling approach allows us to infer changes likely occurring to mid-trophic level organisms through existing knowledge of predators and producers.

2.3 Methods

Study Area

The Hudson Bay region often includes Hudson Bay (HB), James Bay (JB), Foxe Basin (FB) and Hudson Strait (HS) (figure 2.1). This system is one of

2.3. Methods

the largest bodies of water in the world to freeze over every winter and open up every summer. HB and JB are both categorized by shallow, less productive waters, with large inputs of freshwater from rivers in the spring. Conversely, Foxe Basin and Hudson Strait have more mixing with the Labrador Sea (Straneo and Saucier, 2008), and are thought to be an important sea ice choke-point for HB, ultimately determining which marine species have access to the region (Higdon and Ferguson, 2009).

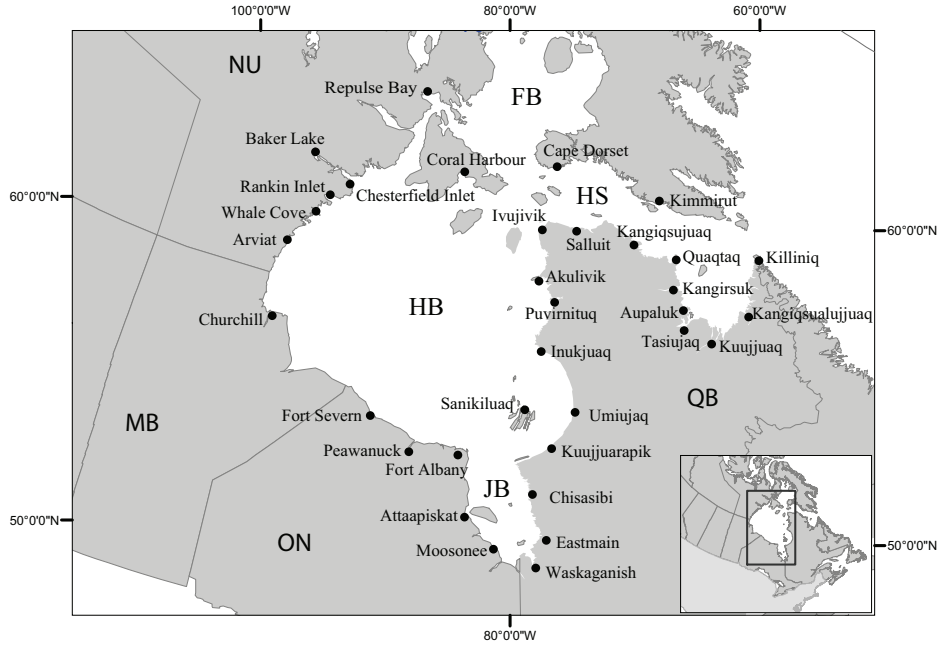


Figure 2.1: Greater Hudson Bay region including Hudson Bay (HB), James Bay (JB), Hudson Strait (HS), and Foxe Basin (FB). Communities in Nunavut (NU), Manitoba (MB), Ontario (ON), and Quebec (QB) are shown.

Selection of the model area was based on use patterns of marine mammals as their data are more prevalent compared to fish and plankton species. JB was included in the model area due to its similarity to southern HB and the use of this area by certain stocks of polar bears, beluga, seals, and birds. HS and FB were excluded from the model area, as these deeper more productive waters are strongly influenced by currents (Straneo and Saucier, 2008), and are likely to host a different suite of species. For the remainder of

this paper, referral to HB will include JB, an area covering roughly 900,000 km^{-2} (Legendre et al., 1996). The Ecopath base year model describes the conditions in 1970, with the Ecosim model running from 1970-2009. The base year was chosen as there are no comprehensive estimates of marine species prior to 1970. In addition, changes in environmental conditions and harvest pressure have been documented for this period, thus making for an interesting time to examine the ecosystem dynamics.

Model Equations

Using the Ecopath with Ecosim (EwE) software version 6 (Christensen et al., 2007; Buszowski et al., 2009), an Ecopath or mass-balance model was constructed for 1970. This mass-balance approach links all species or functional groups (groupings of similar species) through diets. Under this assumption there must be enough energy produced by each prey group to account for consumption, migration, fishing mortality, and other mortalities. More specifically this can be expressed as:

$$P_i = \sum_j B_j \cdot M2_{ij} + Y_i + E_i + BA_i + P_i \cdot (1 - EE_i) \quad (2.1)$$

where P_i is the production of functional prey group i , B_j is the biomass of predator group j with predation mortality on group i of $M2_{ij}$. Y_i is the fishery catch, E_i is the net migration rate (emigration-immigration), BA_i is the biomass accumulation, and EE_i is the ecotrophic efficiency (proportion of production that is consumed within the system by predators or exported out of the system due to fishing or migration) for prey i .

Equation 2.1 can be re-written as equation 2.2:

$$B_i \cdot (P/B)_i = \sum_j B_j \cdot (Q/B)_j \cdot DC_{ji} + Y_i + E_i + BA_i + B_i \cdot (P/B)_i \cdot (1 - EE_i) \quad (2.2)$$

Where B_i and B_j are the biomasses of prey (i) and predator (j), $(P/B)_i$ is the production to biomass ratio, generally equal to total mortality (Z) (Allen, 1971), $(Q/B)_j$ is the consumption by predator j per unit biomass,

2.3. Methods

and DC_{ji} is the proportion of prey i in the diet of predator j . Ecopath models are balanced using an algorithm to solve a set of linear equations in the form of Equation 2.2 for each functional group. For each functional group 3 of the 4 basic parameters are imputed (B, P/B, Q/B, EE) along with fishery landings and diet composition, allowing the algorithm to solve for the 4th parameter.

Temporal simulations were generated for the time period of 1970-2009 in Ecosim using equation 2.3;

$$dB_i/dt = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (MO_i + F_i + e_i)B_i \quad (2.3)$$

Where dB_i/dt represents the change in biomass (B) for group i over the time interval t , with starting biomass B_i . g_i represents the net growth efficiency (production/consumption ratio), the $\sum_j Q_{ji}$ is the total consumption on group i , and $\sum_j Q_{ij}$ is the predation of all predators on group i . MO_i represents the other mortality term (for mortality associated with old age), F_i is the fishing mortality rate, I_i is the immigration rate, e_i is the emigration rate, with the combined term $B_i \cdot (e_i - I_i)$ as the net migration rate. The consumption rate of a group, Q_{ij} is based on the foraging arena theory where the biomass B_i is further divided into vulnerable and invulnerable proportions to group i 's predators (Walters et al., 1997), and the transfer rate between these two states. Ecosim is based on the foraging arena theory that describes the interactions between predators and prey attributing a vulnerability term. Low values of vulnerability (close to 1) mean that prey production determines the predation mortality (bottom-up interaction) while high values of vulnerability (e.g., 100) mean that predator biomass determines how much prey is consumed (top-down interaction)(Christensen and Walters, 2004).

Model Inputs and Functional Groups

Ecopath model parameters were set to 1970 values for the marine environment only, estuary and freshwater areas were excluded from the model. A total of 40 functional groups were created; 15 marine mammal groups, 1 bird group including all birds, 9 fish groups, 7 plankton groups, 4 benthic groups, 2 producers, and 2 detritus groups (species for each functional groups are listed in appendix A with full details on input parameters). Marine mammal groups were created to represent individual species, or separate stocks within species if applicable, as changes in stocks have been identified. As there was little knowledge of fish species in the region, fish species were grouped into functional groups based on life history, feeding preferences, and taxonomic characteristics. Plankton and benthic groups were split into those important to higher predators or groups with more information available.

Primary producers were split into two groups: ice associated algae and pelagic phytoplankton, with the aim to capture the dynamics of organisms, which are dependant on either one. Ice algae is an important component of the ecosystem, as plankton cells are frozen within the ice each fall and released back into the water column during the spring melt. Contribution of ice algae has been estimated at 25% of total production in parts of HB (Legendre et al., 1996) and can range from 57% in the central Arctic to 3% in surrounding sub-Arctic areas (Gosselin et al., 1997). While some species of phytoplankton and zooplankton have adapted to survive this freeze and return to the water column the following year (Horner et al., 1992), those that do not survive sink through the water column to the benthos. Within the model, exports from the ice algae group are directed to the ice detritus group, which is a major contributor to the diets of benthos. During the spring melt, algal cells are flushed out of the brine channels into the pelagic environment, with a minimum export of ice algae to the benthic community estimated at 20% in southeastern parts of HB (Tremblay et al., 1989). Moreover, accumulation of algal biomass within the sea ice is thought to favor an effective transfer to the benthos, as aggregated algal cells sink up to three times faster than individual algal cells, and damaged cells sink

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faster than healthy ones (Tremblay et al., 1989; Riebesell et al., 1991). It has been noted in other Arctic ecosystems that zooplankton biomass is too low during the spring melt to efficiently graze the sinking ice algae, allowing it to sink to the benthos (Legendre et al., 1992).

The pelagic production functional group represents all producers not associated with the sea ice. This group exports to a pelagic detritus groups, which is named as it represents the detritus captured by the pelagic producers, rather than its location in the water column. Pelagic production blooms generally occur after the sea ice has started to melt, and remains in the water column longer than ice algae cells (Tremblay et al., 1989). This pelagic bloom sustains pelagic fish and zooplankton into the summer months.

In order to simulate changes to primary producer functional groups, data was extracted from the global Hadley Centre Sea Ice and Sea Surface Temperature model (HadISST) from the British Atmospheric Data Centre (2010) and used to force the primary production groups. Warmer temperatures have been shown to alter the mean ice freeze-up and break-up dates by 0.8-1.6 weeks in spring and fall (Hochheim et al., 2010). The availability of ice algae within the model is contingent upon the presence of sea ice; therefore the ice algae group was driven through a forcing function (FF) in the model. The sea ice FF was applied to the ice algae group, as a multiplier of the production rate using the average % cover of sea ice of all cells in the model area. The pelagic phytoplankton functional group was also driven in the model using SST (sea surface temperature), from the same HadISST model. Figure 2.2 shows the average SST and % ice cover by month for 1970-2009 with 95% CI. See appendix A for details on model fitting and selection of drivers.

There are no estimates of fish biomass or community composition for HB. Changes in fish populations have been inferred from the diets of thick-billed murre, as biomass is estimated using equations 2.1 and 2.2 in order to satisfy the needs of the predators within the food web, using each group's respective production ability. There has been a shift from Arctic to sub-Arctic fish composition (figure 2.3); from Arctic and polar cod, sculpins, and zoarcids to capelin and sandlance (Gaston et al., 2003). Although the

2.3. Methods

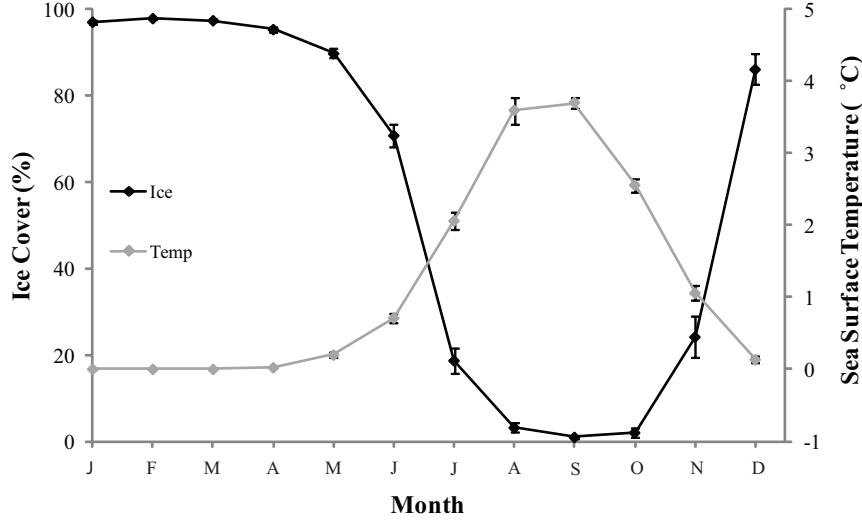


Figure 2.2: 30 year means and 95% CI for sea surface temperature (SST) and % ice cover calculated by the HadISST global model.

diets were collected from the northern limits of HB, due to the gross lack of data on fish populations, diets of birds were the only indication of changes in fish community structure.

For all functional groups biomass parameters were expressed in $t \cdot km^{-2}$, and for non-fish groups were based on surveys collected within the region. For many marine mammal species the total number of animals has been reported. Here, the biomass was extrapolated to the entire region area, which for HB and JB has been estimated at nearly $900,000 km^{-2}$ (Legendre et al., 1996). P/B (production to biomass) and Q/B (consumption to biomass) were calculated as a yearly value (y^{-1}) from species specific empirical values if available, with P/B ratios adjusted to account for hunting and fishing mortality in the Ecopath model. Expert opinion, and values from similar ecosystems were used in absence of region specific data. EE (ecotrophic efficiency) was generally estimated by the model, considering the model balanced when the EE value was between 0 and 1 (Christensen et al., 2005). For full descriptions of data incorporated into the model see appendix A. Model fitting included hunting/fishing for species, which are known to be

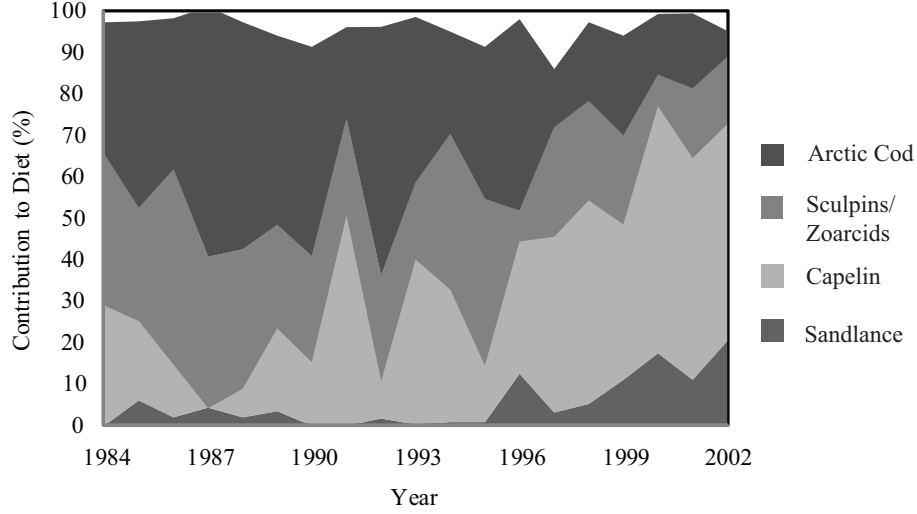


Figure 2.3: Changes in fish abundance as measured by the diets of thick-billed murrelets. Graph recreated from data presented in Gaston et al. (2003).

harvested table 2.1.

Model Analysis and Simulations

Monte Carlo simulations were run on the fitted model to estimate plausible ranges of biomass using equation 2.4:

$$L_{xi} = \bar{x}_i \pm 2 \cdot CV \cdot \bar{x}_i \quad (2.4)$$

where L_x represent the limits (upper and lower) of the biomass of group i . The mean biomass, \bar{x}_i , is taken as the value imputed Ecopath starting value. CV values were determined using a pedigree ranking, whereby input parameters are assigned a coefficient of variation (CV) based on the quality of input data, using the pedigree routine in EwE version 5 (Christensen et al., 2005) (see table 2.2 for CV values used in the Monte Carlo Routine). One thousand Monte Carlo simulations were run to find ranges of input parameters that allowed the Ecopath model to be balanced.

The trophic level (TL) of each species group was calculated for the ini-

2.3. Methods

Table 2.1: Hunting and fishing trends as drivers for the Ecosim model (§ indicates information also contributed by Ferguson (pers. comm.))

Fishery	Functional Groups	Model Drivers	References
SH Polar Bear	Southern Hudson Bay Polar Bear	Landings	(Lee and Taylor, 1994; Aars et al., 2005)
WH Polar Bear	Western Hudson Bay Polar Bear	Landings	(Lee and Taylor, 1994; Aars et al., 2005)
FB Polar Bear	Foxe Basin Polar Bear	Landings	(Lee and Taylor, 1994; Aars et al., 2005)
Killer whale	Killer Whale	Landings	(Higdon, 2007)‡
Bowhead	Bowhead	Landings	(Higdon, 2008)‡
Narwhal	Narwhal	Landings	(DFO, 1990, 1991, 1992, 1993, 1994, 1995, 1996, 1997, 1998; Stewart and Lockhart, 2005; JCNB/NAMMCO, 2009)
N Walrus	Northern Hudson Bay Walrus	Landings	(Strong, 1989; NAMMCO, 2005b; Stewart and Lockhart, 2005)
S Walrus	Southern Hudson Bay Walrus	Landings	(Strong, 1989; NAMMCO, 2005b; Stewart and Lockhart, 2005)
Beluga E	Eastern Hudson Bay Beluga	Landings	(JCNB/NAMMCO, 2009; de March and Postma, 2003)
Beluga W	Western Hudson Bay Beluga	Landings	(JCNB/NAMMCO, 2009; de March and Postma, 2003)
Beluga S	James Bay Beluga	Landings	(JCNB/NAMMCO, 2009; de March and Postma, 2003)
Sealing	Bearded Seal, Harbour seal, Ringed Seal, Harp Seal	Effort	(Stewart and Lockhart, 2005)
Bird Hunting	Birds (all)	Effort	(Stewart and Lockhart, 2005)
Fishing	Arctic Char, Atlantic Salmon, Gadiformes, Sculpins/Zoarcids, Capelin, Sandlance, Other Marine Fish, Brackish Fish	Effort	(Stewart and Lockhart, 2005; Booth and Watts, 2007)

tial Ecopath model and each year of the Ecosim simulation using equation 2.3, where primary producers are assigned a TL of 1, and consumers with diets comprised of 100% primary production have a TL of 2 (Christensen et al., 2007). Consumer TL, TL_i , is dependent upon the TL of prey items (TL_a, TL_b, TL_c , for prey items a, b, c, etc.) and the percentage (X) each prey item contributes to the predator's diet (X_a, X_b, X_c).

$$TL_i = 1 + \sum (X_a * TL_a) + (X_b * TL_b) + (X_c * TL_c)..... \quad (2.5)$$

Once the TL of each species group is calculated, the mean trophic level of the ecosystem (TL_E equation 2.6) and the mean trophic level of the catches (TL_C equation 2.7) can be calculated for each year of the simulations (1970-2009);

$$TL_E = \sum \frac{B_i}{B_E} * TL_i \quad (2.6)$$

$$TL_C = \sum \frac{C_i}{C_E} * TL_i \quad (2.7)$$

where B_i and C_i are the biomass and catch for group i , and B_E and C_E are the biomass and catch of the entire ecosystem, with values represented in $t \cdot km^{-2}$.

Using the model fitted to reported trends in hunting and environmental conditions, further Ecosim simulations were run to test the sensitivity of the ecosystem to hunting and environmental conditions (SST and % ice cover). Two additional simulations were run. First, a "No Hunting" scenario was run, removing all hunting and fishing mortality from the model while still using environmental drivers (SST and ice cover). Second, a "Constant Climate" scenario assumed past hunting levels, but the environmental data from 1970 was repeated annually until 2009, to simulate a constant climate condition thus eliminating the declines in sea ice and increases in temperature. This allowed assessment of climate changes in functional groups if driven by environmental changes, hunting pressure, or both.

2.4 Results

Ecopath Output

Using input parameters listed in appendix A, the model was able to estimate the missing parameters in table 2.2. Through the balancing of the model many parameters were refined. Once Ecopath parameters (B, P/B, Q/B, EE) were calculated, P/B ratios were adjusted to account for hunting mortality. The equation used to calculate the P/B ratio for fish often un-

2.4. Results

derestimates higher latitude species (Pauly, 1980), and the smaller P/B was causing the mass model to estimate large biomasses of fish. Consequently, these ratios were increased to the upper limits based on the species found within the functional group. Many of the zooplankton groups lacked region specific data for P/B and Q/B, therefore a P/Q ratio of 0.25 was assumed (Christensen et al., 2005), allowing the model to estimate an additional parameter. The EE of birds indicated higher mortality than allowed in the model, therefore the P/B ratio was increased to allow for hunting and predation mortality within the model. Food web structure is displayed in figure 2.4.

Table 2.2: Balanced Ecopath model parameters. Biomass (B) and catches are presented in $t \cdot km^{-2}$, PB (Production/Biomass ratio), QB (Consumption/Biomass ratio), and BA (Biomass Accumulation) are presented in y^{-1} . EE (Ecotrophic Efficiency) and P/Q (Production/Consumption) ratios are dimensionless. Bolded values are estimated by the Ecopath model. The CV (Coefficient of Variation) values for each group are used in equation 2.4 to calculate biomass ranges.

Group Name	TL	B	PB	QB	EE	PQ	BA	Catches	CV
WHB Polar Bear	4.857	0.0005	0.129	2.08	0.414	0.062	-	1.50E-05	0.15
SH Polar Bear	4.906	0.0004	0.154	2.08	0.506	0.074	-	2.20E-05	0.15
Polar Bear Foxe	4.927	0.0002	0.121	2.08	0.304	0.058	-	5.00E-06	0.15
Killer Whale	4.872	2.5E-05	0.151	4.998	0.265	0.03	-	1.00E-06	0.15
Narwhal	4.062	0.0019	0.084	26.182	0.271	0.003	-	3.40E-05	0.15
Bowhead	3.335	0.0109	0.021	5.475	0.384	0.004	0.007	9.00E-06	0.4
Walrus N	3.332	0.0027	0.172	47.123	0.188	0.004	-	8.00E-05	0.25
Walrus S	3.452	0.001	0.097	33.778	0.143	0.003	-	6.00E-06	0.25
Bearded Seal	3.866	0.0037	0.176	14.262	0.791	0.012	-	0.000167	0.25
Harbour Seal	3.971	0.001	0.125	18.612	0.074	0.007	-	2.00E-06	0.25
Ringed Seal	4.077	0.0469	0.158	17.272	0.413	0.009	-	0.000393	0.25
Harp seal	4.103	0.001	0.126	15.66	0.688	0.008	-	1.40E-05	0.25
Beluga E	3.694	0.0021	0.066	21.448	0.22	0.003	-0.004	3.30E-05	0.15
Beluga W	3.873	0.0247	0.064	16.713	0.133	0.004	0.01	6.05E-05	0.15
Beluga James	3.869	0.0015	0.087	16.623	0.679	0.005	-	1.40E-05	0.15
Seabirds	3.839	0.065	0.37	17.258	0.95	0.021	-	0.000325	0.4
Arctic Char	3.3	0.412	0.2	1.5	0.95	0.133	-	4.62E-07	0.1
Atlantic Salmon	3.45	0.148	0.52	7.15	0.95	0.073	-	1.32E-08	0.1

Continued on Next Page

Table 2.2 Continued

Group Name	TL	B	PB	QB	EE	PQ	BA	Catches	CV
Gadiformes	3.235	0.853	0.47	1.85	0.95	0.254	-	2.64E-07	0.1
Sculpins/ Zoarcids	3.188	0.382	0.7	3.269	0.95	0.214	-	2.64E-07	0.1
Capelin	3.132	0.488	1.7	4.8	0.95	0.354	-	1.32E-07	0.1
Sandlance	3.128	0.705	0.85	3.45	0.95	0.246	-	3.96E-08	0.1
Sharks/Rays	4.033	3.18E-06	0.22	1.25	0.95	0.176	-	-	0.1
Other Marine Fish	2.948	0.374	0.932	3.018	0.95	0.309	-	6.60E-08	0.1
Brackish Fish	3.216	0.055	3.5	5.798	0.95	0.604	-	2.64E-08	0.1
Cephalopods	3.645	0.227	1.5	5	0.95	0.3	-	-	0.25
Macro-Zooplankton	2.711	7.5	1	3	0.278	0.333	-	-	0.25
Euphausiids	2.787	2.148	3.3	13.2	0.8	0.25	-	-	0.15
Copepods	2.05	4.015	16	64	0.472	0.25	-	-	0.15
Crustaceans	2.41	1.8	3.6	14.4	0.584	0.25	-	-	0.15
Other Meso-Zooplankton	2.336	1.21	10	40	0.556	0.25	-	-	0.15
Micro-Zooplankton	2	2.235	15	45	0.95	0.333	-	-	0.25
Marine Worms	2.275	5.93	0.6	4	0.95	0.15	-	-	0.1
Echinoderms	2.575	8.708	0.3	1	0.95	0.3	-	-	0.1
Bivalves	2.148	5.942	0.57	6.3	0.95	0.091	-	-	0.1
Other Benthos	2.091	3.139	2.5	12.5	0.95	0.2	-	-	0.1
Pelagic Production	1	8	46.865	-	0.8	-	-	-	0.15
Ice Algae	1	3.5	46.197	-	0.65	-	-	-	0.15
Ice Detritus	1	0.009	-	-	0.904	-	-	-	-
Detritus	1	0.33	-	-	0.224	-	-	-	-

2.4. Results

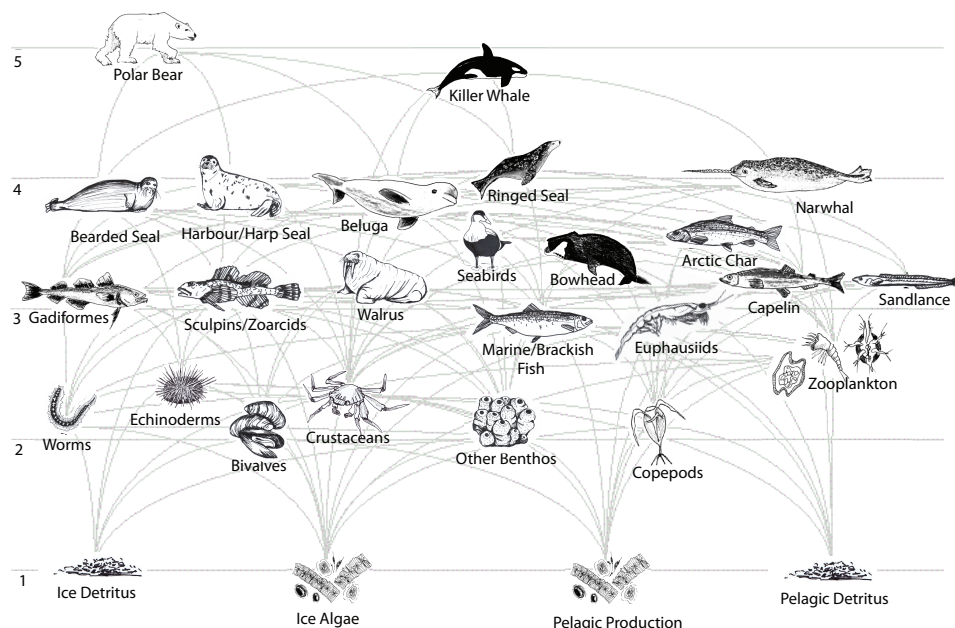


Figure 2.4: Food web linkages in the HB ecosystem with respect to Trophic Level (horizontal lines). Linkages between functional groups were drawn for prey contributing 10% or more to the diet of a predator. For functional groups with more than one species, graphical representation of one species within the group was used. Certain functional groups were combined to be represented by one image; polar bear (western HB, southern HB, and FB polar bear), beluga (eastern HB, western HB, and JB beluga), walrus (northern and southern walrus), harbour/harp (harbour and harp seals), marine/ brackish fish (Atlantic Salmon, sharks/rays, other marine fish, brackish fish), zooplankton (macro-zooplankton, cephalopods, other meso-zooplankton, and micro-zooplankton). Size of image does not indicate biomass size or individual size. All images ©Megan Bailey, 2010 adapted by permission.

Ecosim Fitting

Results of time series fitting, using the data trends provided in table 2.1, and adjusting the vulnerabilities to obtain the observed trends are presented in figure 2.5. See appendix A for full details of vulnerabilities, details of fitting each group, and the general model fitting process. Primary producer groups ice algae and pelagic production were driven with past sea ice and temperature data. Generally, trends for marine mammal functional groups were more easily fit to data, as these time series were created using aerial survey data, and demonstrated gradual changes over time. Data for fitting fish groups provided insight as to general trends of abundance, however the model was unable to simulate the extreme increase in capelin and sand-lance populations indicated by their increase in thick-billed murre stomach content, as well as the full decreases in gadiformes and sculpins/zoarcids as suggested by Gaston et al. (2003). This is caused by the high variability of fish time series as they were compiled from the diets of birds, which demonstrated high annual variability.

James Bay beluga abundance was not able to increase to levels as high as survey estimates implied. While migration from the EHB beluga group (de March and Postma, 2003; COSEWIC, 2004b) was included in the model (through biomass accumulation) and improved the fit for both EHB and James Bay belugas, the model could not capture the full magnitude of the increase. Conversely, a small decline in EHB belugas was created through hunting mortality and vulnerability settings, but was not fully captured until a negative biomass accumulation component was added to the base Ecopath model, accounting for a loss of this population to the James Bay belugas. Bowhead whales were also unable to increase as rapidly within the model, starting at such a low biomass, and a low P/B, thus a biomass accumulation was added to capture this increase, based on known increases to the population as it recovers from whaling (Higdon and Ferguson, 2010). Rates of biomass accumulation are presented in table 2.2, as annual values (yr^{-1}).

Model Results

Although the fitted model cannot fully capture the changes in fish biomass, most notably, increases in capelin and sandlance shifts in fish composition were reflected. Figure 2.6 identifies the changes in fish structure as measured by their percent contribution to the total fish biomass. Since 1970, the model identifies declines in Gadiformes and benthic species (sculpins/zoarcids) along with increases in pelagic-based species (capelin and sandlance), as noted in Gaston et al. (2003). Within the model these changes are driven by the decline in sea ice, and subsequent declines in ice algae and benthos, food sources for benthic feeding fish. However the pelagic based fish (capelin and sandlance) fare much better, as pelagic production increases along with SST. This promotes the pelagic production- pelagic detritus- zooplankton- pelagic fish chain allowing increases in capelin and sandlance.

Monte Carlo simulations (figure 2.7) indicate that the Ecopath model (for the year 1970) can not support higher marine mammal biomasses than the inputted value for most species groups. Ringed seals have the largest starting biomass of any marine mammal group, and also the highest upper limit or largest biomass, which could be supported by the system, followed by WHB beluga and bowhead whales. Ringed seal biomass had a large uncertainty, as population sizes are not well known. However, the model is able to support a large biomass of these seals. Within the model framework, bowheads have the potential to double their biomass while remaining supported by the ecosystem.

2.4. Results

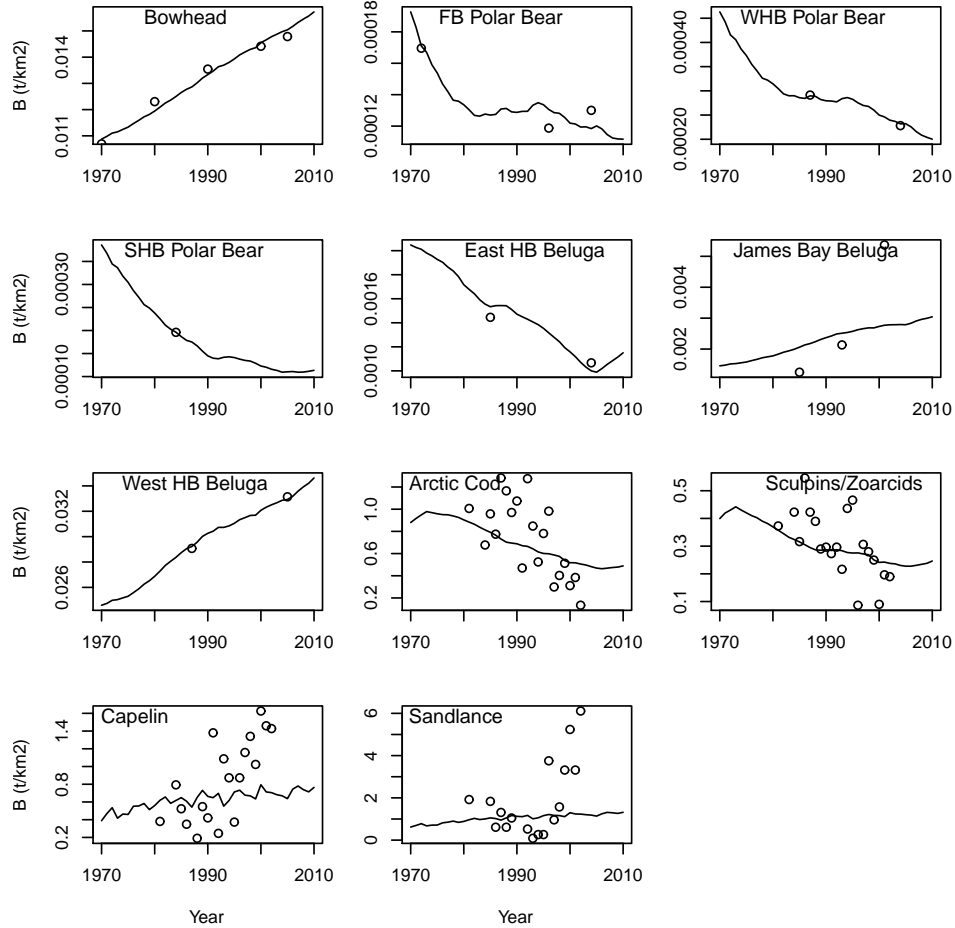


Figure 2.5: Biomass trends for functional groups fitted to time-series data. Solid lines represent model values, while open circles represent observed data points. Data points for each group were taken from: bowhead (Higdon, 2008; Higdon and Ferguson, 2010), polar bears (Lunn et al., 2002; Stirling and Parkinson, 2006), beluga (Hammill, 2001; DFO, 2002a; Gosselin et al., 2002; COSEWIC, 2004a; Gosselin, 2005; NAMMCO, 2005a; Hammill et al., 2009), fish groups (Gaston et al., 2003).

2.4. Results

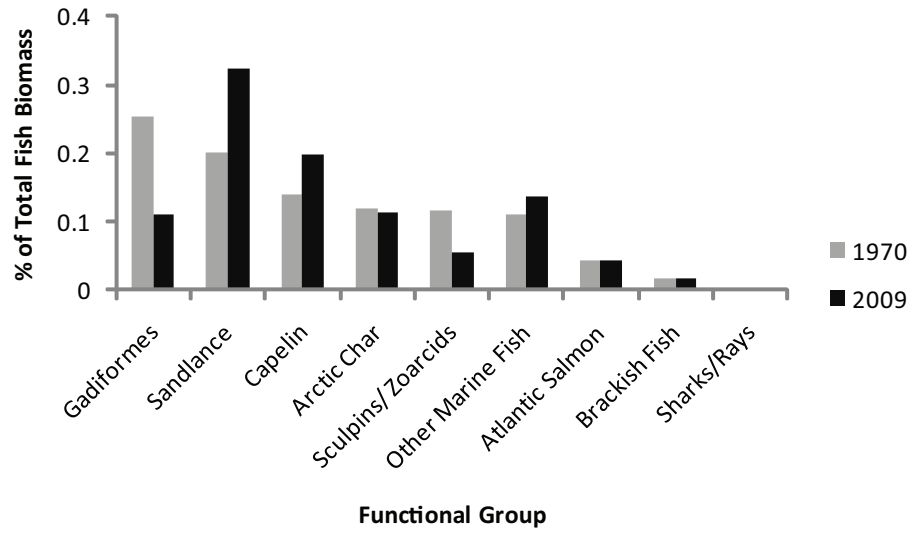


Figure 2.6: Percent contribution of each fish group to total fish biomass using the Ecopath starting biomass ($t \cdot km^{-2}$), and the Ecosim generated biomass for the 2009 value.

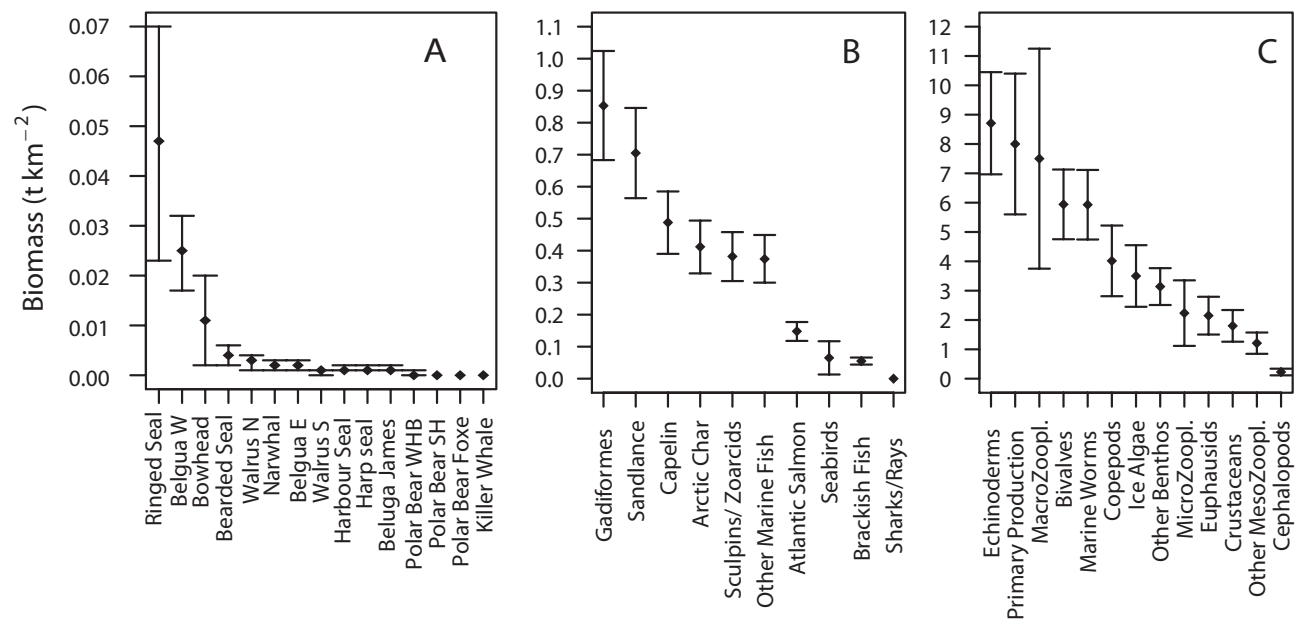


Figure 2.7: Monte Carlo simulation results for Ecopath starting biomass calculated using Eq 2.4. Starting biomass and CV values presented in table 2.2.

2.4. Results

Compared to the inputted biomasses, the ecosystem is able to support higher fish biomasses than the starting value of $3.42t \cdot km^{-2}$ for all fish groups within HB. The total zooplankton biomass of $18.91t \cdot km^{-2}$ falls within the ranges of observed samples, as Harvey et al. (2006) estimated macro and meso-zooplankton from $10-20t \cdot km^{-2}$ for central HB, while a few samples from Harvey et al. (2001) reached close to $50t \cdot km^{-2}$ northern HB.

Table 2.3: Trophic level of the ecosystem (TL_E) and catches (TL_C), presented in 10-year increments. Values were calculated annually from 1970-2009 using Equations 2.6 and 2.7.

Year	TL_E	TL_C
1970	2.457	3.916
1980	2.512	4.033
1990	2.509	4.037
2000	2.541	4.066
2009	2.512	4.032

Trends for trophic levels (TL) of the ecosystem and catches remain relatively stable from 1970-2009 (table 2.3). While catches have a higher trophic level hovering around trophic level 4 (range 3.91-4.07), the ecosystem itself has a much lower trophic level of nearly 2.5 (range 2.45-2.54). This is due to the large proportion of marine mammals being hunted in the system compared to small amount of fish at lower trophic levels. The ecosystem TL remains fairly constant even as declines of polar bears, narwhal, and eastern HB beluga are occurring, as increases in killer whales, seals, and western/JB belugas help to keep the ecosystem TL from declining. While effort for fish, seals, and birds increases based on increases in human populations, these contributions to the overall landings and TL of catches are small in relation to marine mammals, therefore allowing the mean TL of catches to remain high.

Model Simulations

Fitted Model: Past Scenario

Starting from the bottom of the food web, shifts caused by forcing functions were identified. Figure 2.8 (Past Scenario) identifies changes in the ecosystem using the fitted model with past sea ice, SST, and hunting data, as presented in % change from the starting 1970 biomass. Declines in ice algae and ice detritus of nearly 10% each, and increases in pelagic production (26%), and pelagic detritus (33%). Since both the ice algae and the pelagic production groups were forced, these changes were not surprising. Benthos which rely on energy transported from sinking particles, primarily ice algae (Wassmann, 1998; Lavoie et al., 2009), decline under conditions with less ice and ice algae. Zooplankton fare much better, with increases ranging from 12% (micro-zooplankton) to 58% (macro-zooplankton). Although zooplankton consume both ice algae and pelagic phytoplankton, biomass for these groups increases from 12% (micro-zooplankton) to 58% (macro-zooplankton), as the increases in pelagic production are high enough to compensate for the loss of ice algae in the diet.

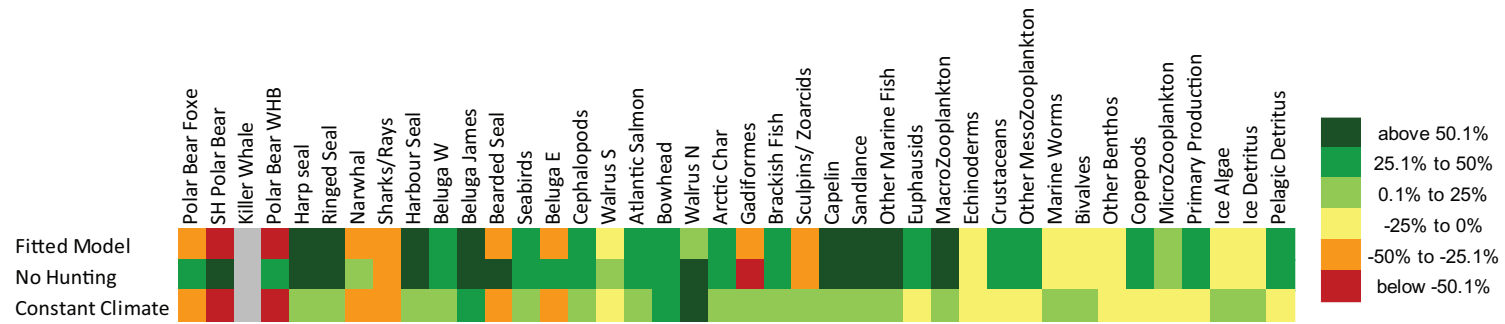


Figure 2.8: Change in biomass from 1970 value under various scenarios: Fitted Model (Fitted model driven using past climate and hunting trends), No Hunting (Model driven with past climate and no hunting), and Constant Climate (Model driven with 1970 climate repeated annually and past hunting). Functional groups are arranged by trophic level, from Foxe Basin polar bears (TL 4.92) to detritus (TL 1)

Declines are identified predominantly in fish with benthic or epibenthic diets (Gadiformes: Arctic and Polar cod, Sculpins/Zoarcids: benthic fish, and sharks/rays) due to declines of ice detritus and other benthos. Gadiformes and sculpins/zoarcids decreased in the diet of thick-billed murres an average of 68% and 57%, respectively, while pelagic-based fish show increases, with the largest being capelin and sandlance (figure 2.3). Fitting of time-series data (figure 2.5) from the diet of thick-billed murres appears to be unable to capture the full magnitude of the increase for both capelin and sandlance.

Most marine mammal groups were fitted to data with the model replicating the trends observed. Polar bears, narwhal, and EHB beluga decline as expected. James Bay beluga, WHB beluga, and bowhead all show increasing trends as identified in model fitting. However, decreases are identified for southern walrus and bearded seals as hunting mortality impact their relatively small populations throughout the simulation. Northern walrus along with harp, ringed, and harp seals show increases in biomass, as hunting mortality is low relative to the population size, and there are decreases to predators (polar bears). The killer whale functional group biomass was based on sightings data (Higdon, 2007), therefore the biomass was not estimated by the model.

Other Scenarios: No Hunting and Constant Climate

Under the No Hunting scenario, all hunting and fishing mortality has been removed, while SST and sea ice were used as environmental drivers as in the past scenario. The biomass of all marine mammal groups increases, with the exception of western and James Bay belugas, which remain the same (figure 2.8). This is due to the relatively low hunting pressure on these specific groups, compared to their biomass. Lower trophic level organisms remain relatively unaffected, as climate is still driving the changes to these groups. Gadiformes are the only fish group to decrease further under this scenario indicating the abundance of marine mammals is causing high levels of mortality on this group.

For the Constant Climate scenario, ice algae and ice detritus show increases compared to other scenarios as expected, however the biomass is quite similar to the 1970 value (<5% increase each), while pelagic production and pelagic detritus show slight declines (close to 10% decrease each). Without the restriction on ice algae, caused by declining sea ice, these changes are propagated through the food web. Increases to benthos are observed as well as declines in zooplankton groups favoring a shift to a more benthic-dominated food web. Fish groups show increases from changes in the lower trophic levels, as well as predator release caused by hunting of marine mammals. Biomass for most marine mammal groups remains quite similar to the fitted model indicating pressures from hunting are a more important factor in determining biomass than climate change.

2.5 Discussion

Fish Biomass and Changes to Fish Composition

While past commercial fishing endeavors have not been profitable (Stewart and Lockhart, 2005), it can be assumed that the region has modest fish biomasses, as Aboriginal communities have harvested fish for thousands of years. This is further corroborated by the ability of the ecosystem to sustain moderate biomasses of fish in the model. Estimates of fish for HB should be considered conservative, as the model only estimates enough fish to satisfy the diets of top predators and fishing, with a total fish biomass estimate of $3.42t \cdot km^{-2}$ for 1970¹. The contribution of each functional group of fish is based on the diets of predators, and the minimum biomass required of each fish group to satisfy the needs of predators. Compared to other regions at similar latitudes this value is still low, but considering the low productivity of the ecosystem it can be considered a plausible estimate. In comparison, fish biomass estimates for other Ecopath with Ecosim models range from

¹This is due to the EE parameter being set to 0.95 for fish species indicating nearly all mortality is caused by fishing and food web interactions

2.5. Discussion

$6.42t \cdot km^{-2}$ to $49.62t \cdot km^{-2}$ for other ecosystems at similar latitudes². As HB is considered oligotrophic (Kuzyk et al., 2011), having a lower cumulative fish biomass than other similar latitude ecosystems is conceivable.

Although there is a general lack of data on trends in fish species, the diet of thick billed murres provides insight as to potential changes occurring within the system. Most notably is the shift from a benthic-dominated system to a pelagic-based ecosystem, demonstrated in the diet of birds as they move from sculpins and zoarcids to pelagic sandlance and capelin (Gaston et al., 2003). Despite the fact that the model fits do not identify the exact patterns for the fish functional groups due to differences in data (figure 2.5)³, changes in composition of fish species are retained (figure 2.6). Declines in the gadiform group stem from the declines in benthic species as prey items. Although the importance of epibenthic prey has been noted in the literature (Craig et al., 1982), in many regions copepods a predominant dietary staple (Sherwood and Rose, 2005). The model diet reflects a larger proportion of benthic prey items (see appendix A) facilitating the decline as climate warms. A re-analysis of the fitted model identifies less severe declines in the gadiform group with increased contribution of copepods and other zooplankton groups to the diet. However, crevasses within sea ice may be important areas for Arctic cod to areas to avoid predators (Gradinger and Blumm, 2004), therefore declines in sea ice would negatively impact Arctic cod. In light of this information, the gadiform group would be expected to decline as demonstrated within the model, albeit possibly with less severity. As the fish data are based on the northern edge of the model region, a greater understanding of fish distribution and diets is important to future modelling. In order to provide more accurate modelling of fish groups, large scale surveys of fish will be necessary for this region. In southern HB, fish may be impacted differently with large freshwater inputs from rivers, causing different environmental conditions.

²Fish biomass pertains to the cumulative biomass of all fish groups within the model. Values from other models at similar latitudes include; 1997 Icelandic shelf model ($17.1t \cdot km^{-2}$) by Samb (1999), 1980 Bering Sea model ($49.62t \cdot km^{-2}$) by Trites et al. (1999), and a 1964 Ionian Sea model ($6.42t \cdot km^{-2}$) by Piroddi et al. (2010).

³Observed changes of fish groups are inputted as the contribution to bird diets

Trophic Level of Catches

The ecosystem is able to sustain a higher mean TL of catches compared to the mean TL of the ecosystem, throughout the model simulation. Fish catches for 1970 totaled 1.14t for the whole model area, much lower than values reconstructed for the Canadian Arctic by Zeller et al. (2011). Per capita consumption rates used to estimate catches were obtained from the same source (Booth and Watts, 2007), however catch reconstruction included fish fed to dog sled teams, which the model presented does not. It is quite possible in reality that catches are higher than the values used in the model, current fishing mortality is low on fish groups indicating they would be able to sustain some increased level of fishing.

While the constant TL of the ecosystem and catches would imply the ecosystem is stable both in its structure and in the composition of catches, it is uncertain if such a high trophic level of catches can be sustained indefinitely. For example, polar bear populations are shown to be declining within the model, and only under scenarios where harvest is included, indicating this level of harvest cannot be sustained. Future reductions of high TL species in the catch composition have the potential to reduce the mean TL of catches over time. This is consistent with ecosystems where fish species have been exploited, a term coined "fishing down the food web" by Pauly et al. (1998a). Hudson Bay is one of a small number of ecosystems worldwide where marine mammal catches provide the greatest contribution to landings of all species, reflected in the high TL of catches. Ultimately, without reductions in catches, populations of marine mammals (such as polar bears) have and will likely continue to decline, thus reducing the TL of the ecosystem. Future simulations are necessary to determine if the current hunting and fishing pressures are sustainable.

Model Simulations

Model simulations (No Hunting, Constant Climate) identified expected responses in the model for most functional groups. Removal of hunting pressure causes increases in targeted species, with little effects to lower trophic

levels. The ability of the ecosystem to withstand increases to the starting biomass ranging from $\sim 6\%$ to $>100\%$ (for narwhal and northern walrus respectively), while not causing declines in fish populations, indicates the ecosystem could support larger biomasses of high trophic level species.

Conversely, simulations with constant environmental drivers (sea ice and SST levels) indicate the sensitivity of producers and lower trophic levels to environmental changes. While producers are driven within the model, their responses mimic higher ice cover and lower SST. Although there are a multitude of factors contributing to primary production such as wind, temperature, light, snow cover, ice cover and nutrient input (Legendre et al., 1996; Gregg et al., 2003; Pabi et al., 2008), in the model higher ice cover facilitates an increase in ice algae, which allows for increased biomass of ice detritus. As this is the main source of detritus for benthos, there is an increase in all benthic groups and continued up to the benthic feeding fish. The decreases in pelagic production, which are assumed to be driven by SST, cause declines in zooplankton groups, and ultimately the fish feeding on zooplankton. The lack of response to higher level predators indicated that this scenario is not severe enough to cause changes to the ecosystem this far up the food web.

Conclusions

Benthic-pelagic coupling of sea ice to ice detritus may be an important factor in determining the abundance of benthic communities. Damaged algal cells from the sea ice sink faster than healthy ones, and increased flushing of algal cells caused by runoff through brine channels in the ice also increase exports (Tremblay et al., 1989). Export of ice algae to the benthic community was estimated at a minimum of 20% in southeastern HB (Tremblay et al., 1989). Moreover, accumulation of algal biomass within the sea ice is thought to favor an effective transfer to the benthos, as aggregated algal cells sink up to three times faster than individual algal cells (Riebesell et al., 1991). It should be noted that the timing of ice melt generally coincides with the pelagic bloom, making for a complex dynamic in benthic-pelagic coupling

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(Smith et al., 2006). The decrease in benthic groups that were observed in the model were impacted by declining sea-ice, yet there are certainly other important factors in the natural environment. In the model, these changes further explain the decreases in benthic fish (as reported from thick-billed murre diets). If the benthic-pelagic coupling was disrupted, it could allow for restructuring of the ecosystem where pelagic species would dominate lower trophic levels.

Zooplankton may not continue to thrive under increasingly warming conditions. As the temperature increases, river runoff and freshwater inputs to the system are also expected to increase, causing both increased nutrients and increased stratification in the water column (Ingram et al., 1996). However, the impacts to the zooplankton community as a whole remain unknown. While ecosystems are resilient, restructuring will occur, potentially replacing marine mammals with larger fish populations.

Through construction and simulations of the ecosystem model, changes to the HB ecosystem can be identified. Decreases to marine mammal populations combined with consistent harvest rates identify the threat to certain populations of top predators. Bottom up changes in SST and sea ice have only been demonstrated to impact the lower trophic levels indicating environmental changes are not yet severe enough to impact marine mammal populations. Even when considering polar bears, where a mediation function was included decreasing foraging habitat as sea ice declined (Stirling and Derocher, 1993). Yet, even with loss of foraging area, hunting mortality was responsible for larger declines in polar bears than climate change.

While ecosystem TL remained relatively constant throughout the fitted model, catches for marine mammal groups (especially cetaceans) cannot be sustained over long periods of time. Certain populations of polar bears, narwhal, and beluga have shown declines causing some to be listed by CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) or COSEWIC (Committee on the Status of Endangered Wildlife in Canada), yet hunting rates have been relatively unaffected. This combined with more extreme future environmental changes, may cause a tipping point in the ecosystem. At some future point environmental changes

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will be great enough to alter food webs, as will declines in top predators. While climate change is relatively unpredictable, it will likely cause future restructuring of lower trophic levels, and potentially the entire food web. Effort to conserving marine mammal populations may prove useful in order to preserve ecosystem structure and prevent the potential over harvest of vulnerable species.

Chapter 3

Effects of Harvest and Climate Change on the Antarctic Peninsula Marine Ecosystem (FAO area 48.1)

3.1 Synopsis

An Ecopath with Ecosim model was created for the Antarctic Peninsula (FAO area 48.1) in order to recreate the past changes to the ecosystem. Declines in krill (*Euphausia superba*) and increases in salps (*Salpa thompsoni*) were recreated based on past data trends, and environmental forcing. Through the use of environmental drivers; sea surface temperature, the Southern Oscillation Index and ice cover, and harvest records, trends from 1978 to 2009 were able to be captured within the model. Environmental variables were tested in different combinations as drivers to assess which variables provided the best fit to observed data. Sea surface temperature was selected over the Southern Oscillation Index as a model driver to producer due to a lower sum of squares value. Large increases in penguin colonies were unable to be captured by the model indicating food web changes do not cause the observed trends, and additional ecological information is needed. Overall declines in sea ice and krill (all life stages) cause large reductions across all trophic levels of the food web, reducing the biomass of nearly all species. Scenarios testing the model sensitivity to environmental drivers and harvest levels identify the ecosystems sensitivity to environmen-

tal changes. Increasing the past catches to the CCAMLR quota level results in minimal differences ($>3\%$ change in biomass) for all species groups when compared to the fitted model using reported catches. Although krill harvest appears to have minimal impacts on the ecosystem within the model, the literature indicates harvest issues may be more sensitive to timing and location of catch rather than total removals.

3.2 Introduction

The Antarctic Peninsula, extending outside of the Antarctic Circle shows milder temperatures than the rest of the continent. It is also one of the fastest warming areas in the world, having an average sea surface temperature (SST) increase of 2.5°C over the last 50 years (Marshall et al., 2006; Rogers et al., 2006), considerably higher than mean global increases (Anisimov et al., 2001; Hansen et al., 2006a). However, other areas of the Antarctic show mixed trends in SST changes, with some increasing and some decreasing (Turner et al., 2005). Polar areas are a major concern for environmentalists as warming will affect ice dynamics, an important feature of high latitude ecosystems.

Since the 1980s there have been many changes to the Antarctic Peninsula, with the collapse of ice shelves as a result of warming. In addition to the breakup of five major ice shelves, warming temperatures have caused glacial retreat of some 244 glaciers over the last 50 years (Doake and Vaughan, 1991; Cook et al., 2005). Moreover, Antarctic ecosystems have a high number of endemic species (Kock, 1992), and their fate in relation to climate change is expected to be serious if these species can not adapt to thermal tolerances. Pole-ward migration is not an option for this region as land barriers prevent movement to higher latitudes.

Krill attracts large quantities of top predators (Howard et al., 2004) and are considered to be a keystone species (Moline et al., 2000), linking most pathways in the food chain from primary producers to top predators. Species of seals, whales, penguins and migratory birds spend varying amounts of time in this region, but are all present in the summer months when pro-

3.2. Introduction

ductivity is highest. All of these top predators are dependent upon Antarctic krill (*Euphausia superba*) at various degrees during the summer months (Doidge and Croxall, 1985; McConnell et al., 1992; Reid and Arnould, 1996; Casaux et al., 1997; Burns et al., 1998; Pauly et al., 1998b; Brierley and Reid, 1999; Tamura and Konishi, 2005). Changes to seal, bird, and baleen whale populations have been linked to changes in climate (Forcada et al., 2005; McMahon and Burton, 2005; Nicol et al., 2008), with the most likely reason being attributed to krill populations. In addition, krill from the Antarctic Peninsula are believed to be a source population to South Georgia (area 48.3), indicating the importance of krill not only to the peninsula, but to surrounding areas and predators at both those locations (Hofmann et al., 1998; Brierley et al., 1999). As krill survival is linked to sea ice through food and protection (Marschall, 1988; Daly, 1990), further warming and loss of sea ice has the potential to impact predators locally and across the Scotia Sea, causing uncertainty in the future of food webs.

Summer abundance of krill in the South Atlantic is positively related to the sea ice extent in the previous winter (Loeb et al., 1997; Atkinson et al., 2004). Algae in the sea ice is an important food source for overwintering krill and new recruits in the spring, when algal biomass is released into the surface waters (Lizotte, 2001; Haberman et al., 2002). Ice is also thought to be used as a shield by krill to protect them from predators (Atkinson et al., 2004). Hence, declining sea ice could have a large impact on krill populations, by removing an important food source, and making the remaining krill more vulnerable to predators.

Although krill are very important in the ecosystem, they can be out-competed in certain years by salps (*Salpa thompsoni*) (Loeb et al., 1997; Atkinson et al., 2004), whose abundance is favored by lower sea ice extent, warmer waters and low to moderate productivity (Nicol, 2006). In warmer years there is less ice algae available throughout winter for krill to graze on, and smaller spring blooms derived from the ice algae lead to poor reproductive success (Marschall, 1988; Loeb et al., 1997; Brierley and Watkins, 2000; Atkinson et al., 2004). In addition, salps are able to take advantage of lower production levels as they are effective grazers, removing carbon from

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the surface and rerouting it to the benthos as faecal pellets (Bruland and Silver, 1981; Pakhomov et al., 2002; Dubischar et al., 2006). Krill on the other hand, are consumed by predators, thereby moving carbon up through the food chain. In addition, warmer, less saline conditions favor the growth of cryptophytes, a producer and important food source for salps (Moline et al., 2000).

The only commercial fishery to remain open in the area at present is for krill. Currently, the krill fishery is open year round with an annual quota of 4 million tonnes for the Scotia Sea (620,000 tonnes for subarea 48.1), while in reality only about 100,000 tonnes are harvested each year primarily in the austral summer (Hewitt et al., 2002). Survival of fledging penguin chicks and Antarctic fur seals is lower in years of low krill abundance (Brierley and Reid, 1999), suggesting that in years of low abundance krill are not always available to predators. Results from a spatial model (Marin and Delgado, 2001) showed that roughly 80% of the krill catch was taken from within penguin foraging areas near the Antarctic Peninsula, suggesting fisheries are in direct competition with predators (Hewitt et al., 2002, 2004), potentially compounding the effects of already low krill biomass in some years. Small Scale Management Units (SSMU) have been considered to further divide the catches from area 48.1 into smaller management areas (Hewitt et al., 2004), however at present this has not been implemented into management (Flores et al., 2011).

An ecosystem model was constructed for the Antarctic Peninsula to gain insight to the factors influencing the dominance of krill or salps, and the changes to the ecosystem which have occurred. The main objectives were to (i) establish a food web model, (ii) identify drivers for krill and/or salp dominance, and (iii) test the ecosystem effects of increasing the harvest of krill from current levels to quota levels.

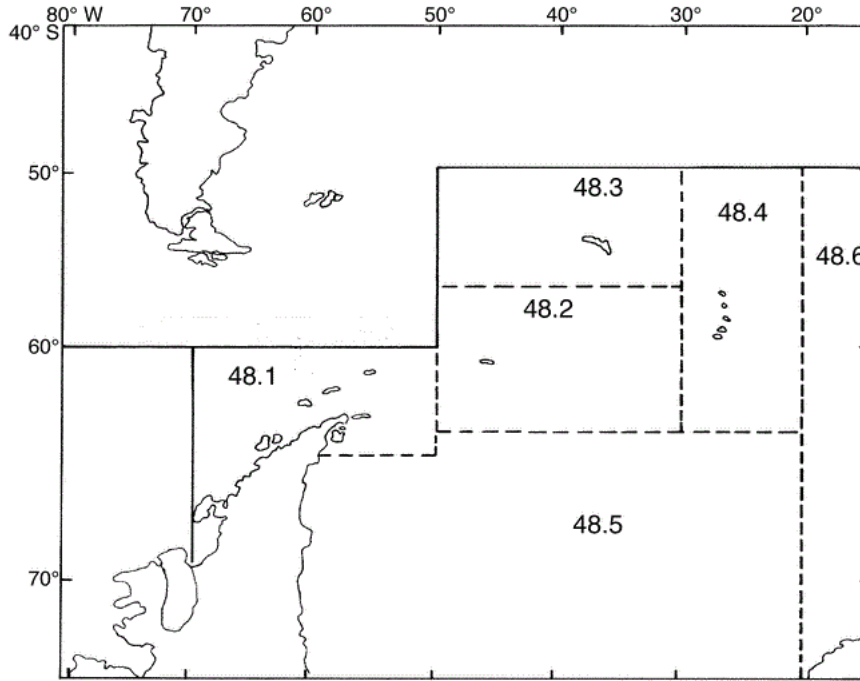


Figure 3.1: Map of Antarctic Peninsula (FAO area 48.1) and surrounding areas. Other areas include South Orkney (48.2), South Georgia (48.3), South Sandwich (48.4), Weddell Sea (48.5) and Bouvet (48.6). The Scotia Sea represents areas 48.1, 48.2, and 48.3 combined.

3.3 Methods

Study Area

For the model the Antarctic Peninsula statistical area (FAO area 48.1) was selected as the model area (figure 3.1). The peninsula has a highly productive shelf zone (Smith et al., 1998) which attracts migratory species in addition to the year round inhabitants. It contains both continental shelf and deeper basin waters constrained by the ACC (Antarctic Circumpolar Current) which flows around the continent keeping cold water close to the shelf and warmer waters offshore. These highly productive waters encourage high populations of krill biomass (Atkinson et al., 2008), which in turn draws high numbers of migratory species to the area selected. Selection of

model area was chosen primarily based on available data. While the Bellingshausen Sea to the west has also demonstrated changes in climate (Abram et al., 2010), and South Orkney and South Georgia to the east are on the receiving end of krill being transported via currents (Hofmann et al., 1998), they were both excluded from the model. Data provided by CCAMLR is compiled by statistical area (CCAMLR, 2008a), and while high numbers of predators are present at South Georgia additional sub-Antarctic species groups would need to be included, thus expanding the food web further. The Bellingshausen Sea does not attract such high abundances of top predators as the peninsula, in addition to less data being available for this area. Thus, only subarea 48.1 was selected as the model area.

All animals spending time in the region were included in the model. The model was selected to start in 1978. Krill and salp data were available starting from this time (Atkinson et al., 2004) in addition to penguin data for the 1980s (Fraser, 2006). While there was one year of reported catches for krill before 1978 (1976 389t), no indication of biomass was available pre-1978, so this was selected as the starting year of the model.

Model Equations

Methods for creating the model were consistent with chapter 2, using the Ecopath with Ecosim approach (Christensen et al., 2005, 2007). Ecopath Equations 1 and 2, and Ecosim equation 3 remain unchanged from the previous chapter. The model was considered balanced when all Ecotrophic Efficiencies (EE) values were between 0 and 1. For the Ecosim portion the fitting of the model was accomplished through the inclusion of time series data (catches and abundance trends) in addition to environmental parameters; sea surface temperature (SST), ice cover and the Souther Oscillation Index (SOI). The automated fit to time series routine (Christensen and Walters, 2004; Christensen et al., 2005) was used to assist in providing estimates of vulnerability parameters. A default value of 2 indicating a mixed relationship (neither top-down or bottom-up) was used to start the fit to time series routine. Low vulnerability values (close to 1) indicate a bottom-up

relationship between predators and prey, while higher values (close to 100) indicate a top-down relationship. Once the automated search routine was completed, the vulnerabilities were further manipulated manually to lower the sum of squares (SS) value. The model was considered fitted when further alterations to vulnerabilities or other parameters failed to reduce the SS value.

Model Inputs and Functional Groups

Input parameters for Ecopath were set to 1978 values for all species inhabiting area 48.1. 59 functional groups were created; 12 marine mammal groups, 5 penguin groups, 1 flying bird group, 12 fish groups, 15 benthic groups, 9 zooplankton groups, 4 phytoplankton groups and 1 detrital group. Migratory and year round residents of marine mammals were included in the model. Baleen whales spend their summer months in the model area, where they consume a large portion of their annual food intake (Best and Schell, 1996; Schell et al., 1989). In order to compensate for feeding outside the model area, the biomass of baleen whale groups was adjusted to 75% of their peak summer biomass to account for 75% of their annual food intake from within the model area, as migratory whales have been shown to feed outside of summer feeding habitats (Schell et al., 1989). Fish groups were separated based on feeding patterns, depth ranges, size and familial characteristics. Benthic groups were created based on abundances from survey samples and importance to predators. Zooplankton groups were divided into 4 krill groups (representative of different age classes), salps and various other zooplankton species important to krill and higher predator diets. The producers were split according to the conditions which favor them (warm years or cold years). One detritus group was created to represent all detritus. Appendix J provides a detailed description of all species groups.

Primary producers were split into four groups in order to account for their different roles in the food web; ice algae, diatoms, cryptophytes, and other phytoplankton. Research has identified linkages between cryptophyte blooms and lower salinity water, as well as diatoms and higher salinity wa-

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ters (Moline et al., 2000, 2004). Diatoms and cryptophytes have been shown to be the dominant phytoplankton for the region in the summer months with diatoms having a strong association with sea ice (Varela et al., 2002; Garibotti et al., 2003; Moline et al., 2004), thus demonstrating their importance to the food web. Diatoms are also favored in cooler years associated with higher sea ice, and are often an important component of sea ice algae, forming blooms at the ice edge when melting commences (Legendre et al., 1992). Ice algae remain in the sea ice overwinter and are utilized by predators such as krill throughout the winter (Marschall, 1988; Arrigo et al., 1997).

Krill and salps were given their own functional groups within the model, with krill broken down into four levels each representing a different life stage (see krill summary in appendix J for further details). The krill stages chosen for the model were: (i) Krill eggs (eggs are spawned and sink to depths before ascending to reach food (Marr, 1962; Hofmann et al., 1992; Nicol et al., 1995; Reid, 2001)), (ii) larval krill (first feeding stage where food is critical, and the availability of phytoplankton is paramount (Ross and Quetin, 1986)), (iii) juvenile krill (physically resemble adults, but are sexually immature), and (iv) adult krill (sexually mature krill that are targeted by predators and the krill fishery (Lowry et al., 1998; Jones and Ramm, 2004)). One group was created for salps to represent solitary and colonial forms (Foxton, 1966).

Surveys of benthos (Jazdzewski et al., 1986; Saiz-Salinas et al., 1998; Piepenburg et al., 2002) and fish (Daniels and Lipps, 1989; Frolkina et al., 1998; Kock, 1998; Arana and Vega, 1999; Barrera-Oro et al., 2000; Jones et al., 2000; Kock and Jones, 2005) provided samples from a variety of depths and areas. These were combined with peer-reviewed literature (appendix J) to obtain parameter values for benthic and fish functional groups. Penguin and marine mammal information for the entire region was scarce. However, surveys in time or space provided insights in population sizes and trends (Hunt, 1973; Gilbert and Erickson, 1977; Laws, 1977; Whitehouse and Viet, 1994; Boyd et al., 1998; Gelatt and Siniff, 1999; Leaper et al., 2000; Quintana et al., 2000; Branch and Butterworth, 2001; Fraser, 2006; Secchi et al., 2006; Williams et al., 2006). In many cases values from either the whole Antarctic or a small specific region of the model area were used to extrapolate values

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for area 48.1. Parameters for all functional groups within the model were set to values averaged over the entire model area.

For area 48.1 the total area was set to 672,000 km^2 (CCAMLR pers. comm. 2007). Biomass values ($t \cdot km^{-2}$) were taken from surveys and converted from abundance using average weights, and total model area if necessary. Production and consumption parameters (P/B and Q/B) were calculated from empirical equations or taken directly from literature if available. These required species specific equations found in appendix J, calculated as annual values (y^{-1}). Diets were available from literature for most species. On occasion parameter values were inferred from similar species, or when values could not be reasonably estimated. The Ecotrophic Efficiency (EE) was left blank for most groups to be estimated by the model. Adjustments to the model during the balancing and fitting processes primarily included changes to diet, with some adjustments to P/B, Q/B. The model was considered balanced when all EE values were between 0 and 1 (Christensen et al., 2005). For a detailed description of the model parameters and calculations please refer to appendix J.

Table 3.1: Time series data used for model fitting. Data sources and type of data used is noted.

Time series data	Type of data used	Reference
Krill Abundance	Relative Abundance	Atkinson et al. (2004)
Krill Catch	Forced Catches	CCAMLR (2008a)
Krill Effort	Effort	CCAMLR (2008a)
Salp Abundance	Relative Abundance	Atkinson et al. (2004)
Other Fishery Catch	Forced Catches	CCAMLR (2008a)
Other Fishery Effort	Effort	CCAMLR (2008a)
Adelie Penguin Abundance	Relative Abundance	Fraser (2006)
Gentoo Penguin Abundance	Relative Abundance	Fraser (2006)
Chinstrap Penguin Abundance	Relative Abundance	Fraser (2006)

The model fitting process in Ecosim incorporated catches of krill and fish (figure 3.2) from CCAMLR data ranging from 1978-2007 (CCAMLR, 2008a), along with environmental drivers including sea ice, SOI and SST in an attempt to recreate changes recorded in the past. A summary of all abundance trend data used for the model fitting for functional groups is provided in table 3.1. Sea ice and SST data were extracted from the HadISST global

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model by the British Atmospheric Data Centre (BADC, 2010), while the SOI was taken from the PALMER LTER (Long Term Ecological Research) (Stammerjohn, 2007). The ice cover forcing function (FF) was used as a driver for the ice algae and diatom functional groups. Ice algae remain in the sea ice overwinter and are utilized by predators such as krill throughout the winter (Marschall, 1988; Arrigo et al., 1997). Diatoms are favored in cooler years associated with higher sea ice, and are often an important component of sea ice algae, forming blooms at the ice edge when melting commences (Legendre et al., 1992). In addition sea ice was used as a FF for ice algae predators, applied to the arena area for each predator. The ecological interpretation is that as ice cover increases, so does the arena area for predators to feed on ice algae.

SOI⁴ and SST were used under different fitting attempts (A and B respectively) for cryptophytes and the other phytoplankton functional groups. This is due to cryptophytes having higher biomass in warmer years (Moline et al., 2004), and the other phytoplankton group representing species associated with the spring bloom. The annual SST pattern has a similar pattern to summer blooms during ice free conditions. FF of cryptophytes and other phytoplankton were chosen to help fit the salp functional group, which is able to tolerate warmer water than krill (Atkinson et al., 2004). The SOI was tested in the model as salps abundance has been linked to the SOI (Loeb et al., 2009).

Mediation functions were also used in the fitting of the model to represent indirection interactions between species groups. For example, as krill have been observed by SCUBA divers to retreat into crevasses in sea ice for protection (Marschall, 1988), a mediation function between krill and their predators was created. As the biomass of ice algae increases, krill become less vulnerable to their predators, with a large decline as ice decreases from

⁴The Southern Oscillation Index (SOI) used in the model is calculated using the difference in air pressure between Tahiti and Darwin, Australia. Positive values indicate cold ocean temperature, higher air pressure in Tahiti, and lower air temperature in Darwin. Negative values indicate, lower air pressure in Tahiti, higher air pressure in Darwin, and warmer waters. Positive values are generally associated with La Nina years, while negative values are associated with El Nino years.

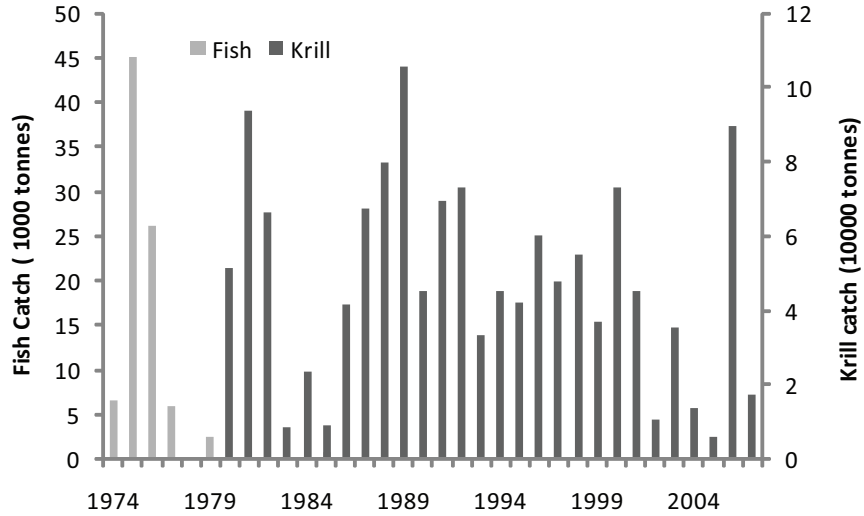


Figure 3.2: Krill and fish catches presented by year. Data was extracted from the CCAMLR online database (CCAMLR, 2008a).

the starting values within the model, and tapering impacts from low to extremely low ice cover⁵. This mediation function was applied to both the larval and juvenile stages of krill under both fitting scenarios (SOI and SST). As salps are pelagic organisms with the abundance higher in warmer years with lower sea ice (Moline et al., 2004; Nicol, 2006), the mediation function used indicated as sea ice decreased (as determined by ice algae), the foraging area of salps increased using a linear relationship⁶. This mediation function was applied to all prey groups of salps under both fitting scenarios (SOI and SST).

Other environmental time series were tested in the fitting of the model, but did not produce optimal results. Data from the PALMER LTER study of sea ice extent, open water extent and air temperature were considered (Stammerjohn, 2007). Selection of the fitted model was based on the lowest sum of squares (SS) value in addition to the model representing past data.

⁵This interaction was fit to a sigmoid curve. Figure and starting points are shown in appendix J

⁶See appendix J for figure

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While sea ice extent did provide comparable results to the ice cover FF (forcing function) (once both FF were rescaled to average 1 for the first year), future data is available for percentage ice cover, therefore it was selected over ice extent. In addition, a clogging function for salps was employed to reflect the clogging of mucous nets in areas of high particle concentration. This has been shown to occur for some species of salps in lab experiments, and is believed to be the cause of a mass stranding of *Salpa thompsoni* near the Antarctic Peninsula in 2002 (Harbison et al., 1986; Pakhomov et al., 2003). The mediation function was applied to the search rate of salps on other phytoplankton and cryptophytes, so as the biomass of other producers increase, the search rate will also increase to a certain point and then drop off. While this mediation function did improve the SS value initially, the sea ice mediation function provided a lower SS value. The combination of both mediation functions of salps did not provide a lower SS value than the sea ice mediation function alone, so the clogging function was removed from the model.

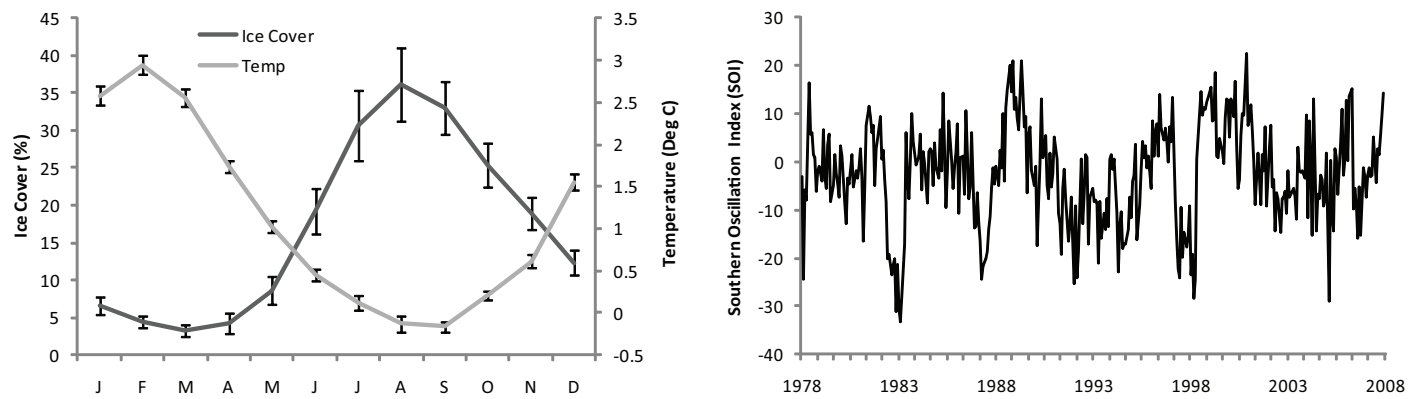


Figure 3.3: Environmental drivers used in the model fitting process. Sea surface temperature (SST) and sea ice are presented as mean values with 95% CI to show annual patterns. Southern Oscillation Index (SOI) is presented as a timeseries to identify positive and negative years.

Model Analysis and Simulations

Once the model was fit to data, Monte Carlo simulations were used to estimate the range of acceptable input parameters, specifically biomass. Equation 2.4 from chapter 2 was used in the same manner as for the Hudson Bay model. The Ecopath input value for each functional group was used as the mean value with the CV (Coefficient of Variation) values for biomass parameters presented in table 3.2. CV values were determined by pedigree ranking routing, whereby uncertainty in input parameters is determined based on the quality or source of the value (Christensen et al., 2005). Mean trophic level (TL) of the ecosystem, and catches were calculated using equations 2.6 and 2.7 from chapter 2. Producers and detrital groups are set to a TL of 1, with the rest of predators calculated based on diets.

Two models using SST and SOI to drive the warmer phytoplankton species (cryptophytes and other phytoplankton) showed comparable results for most species groups. However, the SST model was ultimately selected and used for simulations. Simulations testing the model sensitivity to drivers were applied to the fitted model. The first "Constant Climate" scenario tested the sensitivity of the model to climate drivers, by removing changes throughout time. The SST and ice cover patterns from 1978 were replicated to mimic constant climate over time. Under this scenario hunting trends were maintained to represent past catches. Next a "Harvest Quota" scenario applied the krill quota as the level of catch for krill each year of the simulation in combination with past environmental drivers. While the krill fishery operates lower than the quota limit of 625,000 tonnes for area 48.1 (Hewitt et al., 2002), the potential effects to the ecosystem if the fishery had operated at quota levels of harvest were explored.

3.4 Results

Ecopath Output

In the Ecopath phase, changes were made to parameters in order to ensure the model could be balanced before moving onto the Ecosim portion.

3.4. Results

General changes to Ecopath parameters were made in order to balance the model. Calculated consumption rates of marine mammals were high in some cases and had to be decreased to prevent EE for prey groups from going over 1. In most cases the Q/B value reduction was small (less than 10% of the initial value). The P/B ratios for fish groups calculated by equations in Pauly (1980) were too low. As the empirical data used to formulate this equation was based on temperate and tropical fish species and excluded polar data, it most likely underestimates the value for polar species (Palomares and Pauly, 1998). P/B values were increased to balance the fish groups and the rest of the model. Next, literature indicates a very strong dietary link between predators and krill. However, even though krill biomass was large in comparison to other zooplankton (48% of total zooplankton biomass including salps for all stages of krill), the contribution to the diet of predators had to be decreased in order to balance the model. Finally, changes were made to the P/B and Q/B values for invertebrates. Most alterations made to calculated values were increases in order to balance the model, to provide enough prey for fish and pinniped groups. In addition to these general parameter changes, smaller adjustments were made to diets in the fitting process to better capture past trends. Final model parameters available in appendix J are presented as the values used for the balanced model, with parameters adjusted during the fitting process indicated the table 3.2.

Table 3.2: Balanced Ecopath model parameters. Biomass (B) and catches are presented in $t \cdot km^{-2}$, PB (Production/Biomass ratio), QB (Consumption/Biomass ratio), and BA (Biomass Accumulation) are presented in y^{-1} . EE (Ecotrophic Efficiency) and P/Q (Production/Consumption) ratios and TL (Trophic Level) are dimensionless. Bolded values are estimated by the Ecopath model. The CV (Coefficient of Variation) values were used to calculate biomass ranges for Monte Carlo routine.

Group Name	TL	B	PB	QB	EE	PQ	BA	Catches	CV
Killer Whales	4.543	0.001	0.050	11.000	0.000	0.005	-	-	0.7
Leopard Seal	4.139	0.006	0.120	8.100	0.637	0.015	-	-	0.7
Ross Seal	4.123	0.004	0.130	15.300	0.830	0.008	-	-	0.4
Weddell Seal	3.972	0.021	0.170	13.880	0.689	0.012	-	-	0.7
Crabeater Seal	3.423	0.164	0.090	15.860	0.363	0.006	-	-	0.7
Antarctic Fur Seals	3.694	0.028	0.175	25.000	0.862	0.007	-	-	0.7
S Elephant Seals	4.250	0.006	0.165	10.370	0.437	0.016	-	-	0.7
Sperm whales	4.203	0.005	0.034	7.330	0.000	0.005	-	-	0.7
Blue Whales	3.410	0.001	0.032	3.530	0.683	0.009	-	-	0.7
Fin Whales	3.441	0.003	0.035	4.120	0.524	0.008	-	-	0.7
Minke whales	3.270	0.065	0.064	6.340	0.910	0.010	-	-	0.7
Humpback whales	3.343	0.020	0.040	4.120	0.963	0.010	-	-	0.7
Emperor penguins	3.871	0.005	0.150	28.690	0.933	0.005	-	-	0
Gentoo Penguins	3.930	0.007	0.220	29.000	0.642	0.008	-	-	0.7
Chinstrap Penguins	3.917	0.005	0.330	34.000	0.696	0.010	0.057	-	0.7
Macaroni Penguin	3.670	0.014	0.300	25.000	0.373	0.012	0.100	-	0
Adelie Penguins	3.518	0.034	0.290	30.000	0.793	0.010	-	-	0.7
Flying birds	3.697	0.190	0.340	14.880	0.950	0.023	-	-	0.4

Continued on Next Page

Table 3.2 Continued

Group Name	TL	B	PB	QB	EE	PQ	BA	Catches	CV
Cephalopods	3.404	2.490	0.950	2.000	0.653	0.475	-	-	0.4
Other Icefish	3.689	0.337	0.380	1.570	0.726	0.242	-	1.00E-05	0.7
Toothfish	4.228	0.046	0.165	0.770	0.627	0.214	-	1.00E-05	0.7
Lg Nototheniidae	3.335	0.590	0.370	1.950	0.452	0.190	-	1.00E-05	0.7
Sm Nototheniidae	3.332	0.341	0.650	2.200	0.873	0.295	-	1.00E-05	0.7
Shallow Demersals	3.375	0.031	0.750	4.125	0.362	0.182	-	-	0.7
Deep demersals Lg	3.684	0.042	0.290	2.180	0.803	0.133	-	-	0.7
Deep demersals Sm	3.687	0.080	0.650	2.700	0.820	0.241	-	-	0.7
Myctophids	3.263	0.185	1.350	3.730	0.882	0.362	-	1.00E-05	0.7
Other Pelagics	3.776	0.490	0.550	2.020	0.838	0.272	-	1.00E-05	0.7
C gunnari	3.391	0.290	0.480	1.800	0.475	0.267	-	1.00E-05	0.7
P antarcticum	3.269	1.250	1.100	3.550	0.603	0.310	-	1.00E-05	0.7
N gibberifrons	3.199	0.810	0.410	1.550	0.645	0.265	-	1.00E-05	0.7
Mollusca	2.129	9.500	0.639	2.556	0.608	0.250	-	-	1
Salps	2.227	8.000	10.000	33.333	0.010	0.300	-	-	1
Urochordata	2.135	5.050	0.234	1.000	0.554	0.234	-	-	1
Porifera	2.000	12.719	0.159	0.795	0.815	0.200	-	-	1
Hemichordata	2.000	0.045	0.375	2.000	0.534	0.188	-	-	1
Brachiopoda	2.158	0.028	0.898	4.500	0.590	0.200	-	-	1
Bryozoa	2.108	0.491	0.475	1.750	0.980	0.271	-	-	1
Cnidaria	2.438	1.531	0.250	1.000	0.982	0.250	-	-	1
Crustaceans	2.374	3.613	1.050	4.200	0.888	0.250	-	-	1
Other Arthropods	2.929	1.010	0.616	3.326	0.981	0.185	-	-	1
Worms	2.438	12.000	0.700	3.200	0.840	0.219	-	-	1

Continued on Next Page

Table 3.2 Continued

Group Name	TL	B	PB	QB	EE	PQ	BA	Catches	CV
Echinoidea	2.732	4.330	0.116	0.464	0.774	0.250	-	-	1
Crinoidea	2.428	0.164	0.125	0.800	0.523	0.156	-	-	1
Ophiuroidea	2.479	6.760	0.450	1.800	0.551	0.250	-	-	1
Asteroidea	2.345	1.778	0.231	0.924	0.774	0.250	-	-	1
Holothuroidea	2.000	5.450	0.316	1.100	0.938	0.287	-	-	1
Krill Adult	2.529	9.080	1.500	33.000	0.672	0.045	-	0.055	1
Krill Juvenile	2.250	25.260	0.900	49.481	0.788	0.018	-	0.018	1
Krill Larvae	2.000	0.879	2.500	149.443	0.011	0.017	-	-	1
Krill Embryo	2.000	0.006	8.000	698.506	0.237	0.011	-	-	1
Macro-Zoopl	2.154	8.170	7.577	25.257	0.950	0.300	-	-	0.7
Micro-Zoopl	2.000	2.900	65.000	110.000	0.982	0.591	-	-	0.7
Cryptophytes	1.000	2.200	80.000	0.000	0.983	-	-	-	0.4
Copepods	2.150	15.200	26.066	50.000	0.950	0.521	-	-	0.7
Diatoms	1.000	17.410	90.510	0.000	0.396	-	-	-	0.7
Ice algae	1.000	25.000	45.000	0.000	0.874	-	-	-	0.7
Other Phytopl	1.000	5.500	105.000	0.000	0.806	-	-	-	0.4
Detritus	1.000	3.430	-	-	0.176	-	-	-	-

Continued on Next Page

Ecosim Fitting

The model was fit under 2 conditions: The first fitting used SOI to drive cryptophytes and the other production group, and the second fitting used temperature (SST) as a forcing function for cryptophytes and other production. Both fitting scenarios used ice cover (% of model area covered with ice) as a FF for the ice algae and diatom functional groups. In addition, both fitted models incorporated mediation functions allowing young krill (larval and juvenile stages) increased protection from predators at higher sea ice concentrations, and salps a smaller foraging area as sea ice increases (please refer to appendix J for a full description of forcing and mediation functions).

For both attempts at fitting the model, there was no difference to the fit of penguin groups. Declines in Adelie penguins were captured through the decline of the main prey item krill. For the chinstrap and gentoo penguins, obtaining increases in the population while food sources (krill, cephalopods, and fish) declined was not possible. However, based on increases in both populations documented, biomass accumulation rates of $0.10y^{-1}$ and $0.057y^{-1}$ were added for chinstrap and gentoos respectively. For gentoo penguins this was based on increases of 5.7% at Cierva Point on the Antarctic Peninsula, and a nearly 50 fold increase at PALMER Station on Anvers Island (Quintana et al., 2000; Fraser, 2006). Chinstrap penguin trends identify increases in breeding pairs from 28 to 1288 between 1996-2004 at PALMER Station (Fraser, 2006) and increases in colonies ranging from 6-10% per year for specific areas within the model area (Fraser et al., 1992). However, these trends of large increases are not indicated to hold true outside of these specific study sights.

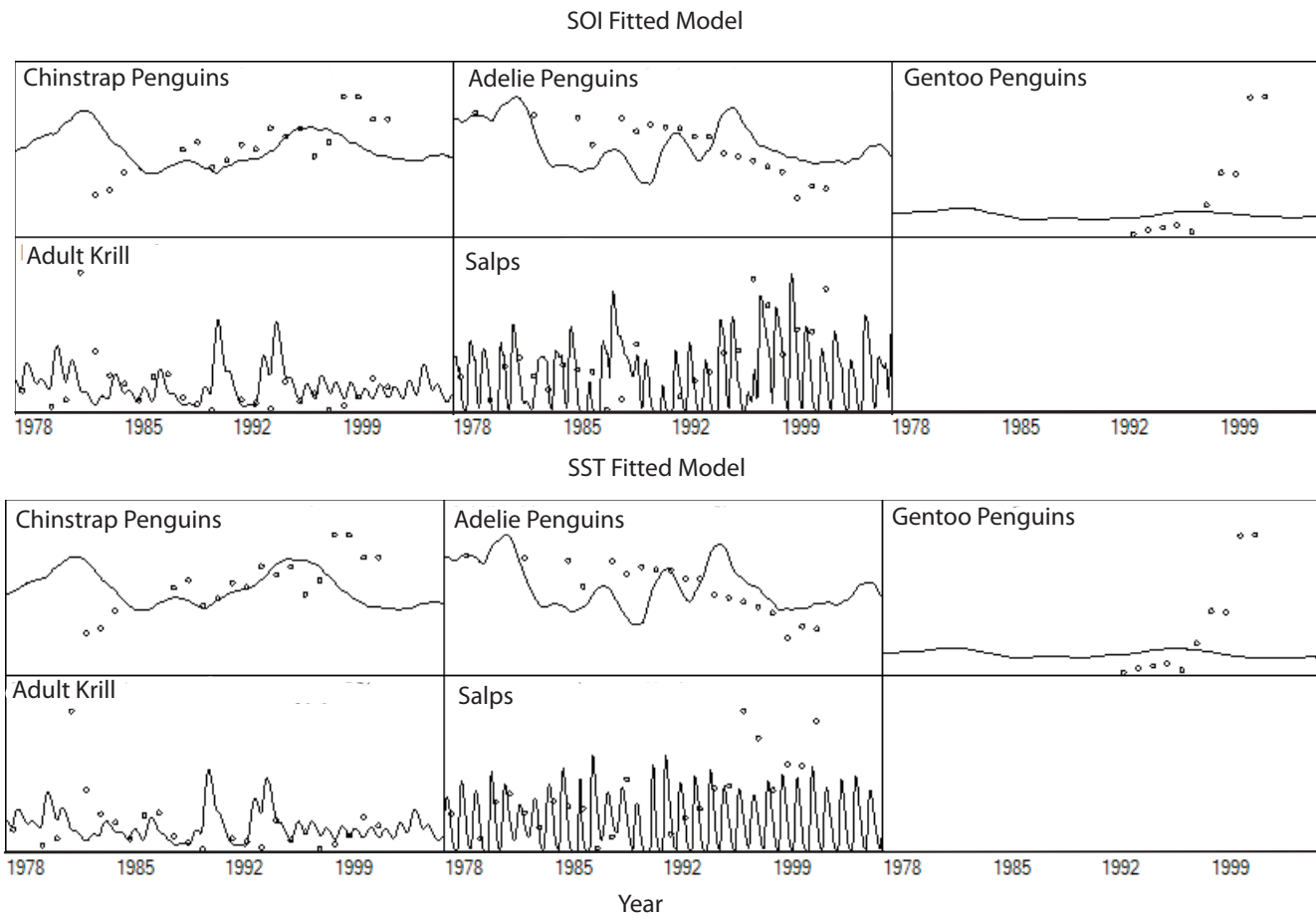


Figure 3.4: Model fitted to data for the Antarctic Peninsula using data trends from table 3.1. Data for the SOI fitted model (top) and the SST fitted model (bottom) remain the same, only different forcing functions were used as model drivers.

3.4. Results

Krill were fit to the model using the mediation function for sea ice (see appendix J), and through the use of sea ice as a driver of their main food sources, sea ice algae and diatoms in addition to protection from predators. Krill abundance has been shown to be higher in years with lower sea temperature, higher sea ice extent, and higher nutrient concentrations, while the opposite patterns are observed for salps (Lee et al., 2010). Although the peak in biomass for 1983 was not captured in the model for adult krill, juvenile krill show a higher biomass than adult krill in this year. While some juvenile krill are likely caught in the samples provided by this dataset, as the adult group is classified by sized 35mm and larger, neither group shows the highest biomass in this year. The highest adult krill biomass is shown in the model for 1992 at just over $23t \cdot km^{-2}$ while the highest biomass for juveniles was in 1988 at just over $58t \cdot km^{-2}$, the highest biomass projected by the model for any krill group. Krill trend data from observations indicates high biomass in 1992 and 1996, although adult krill in the model does not show high biomass in these years. Juvenile krill shows a relatively high biomass in 1996, but not 1992.

The greatest differences between the two fitted models arises from the groups where SST and SOI were used as forcing functions: cryptophytes and the other phytoplankton group. For cryptophytes, both models show peaks in abundance in 1987 and 1992, however values are higher under the SST fitted model. The other phytoplankton group shows the same general trends for both fitted models, however peak abundances are higher under the SST fitted model, and low values are more extreme under the SOI fitted model. These differences influence the salp group which shows different trends under both fittings. Under the SST fitted model a peak in salp biomass for 1989 is lower than for the SOI fitted model. Also the SOI fitted model generally has higher salp biomass values after 1999 compared to the SST fitted model. The ending biomass for the SOI fitted model is higher for the salp group. While the SOI fitted model visually appears to fit the salp trend data better, it has been suggested recently in the literature that salp trends from 1998 onward are thought to have stabilized showing mid range abundances in recent years when compared to data from 1975-2002 (Lee et al., 2010). This

is different from the data used for the model (Atkinson et al., 2004) which still shows fluctuations in salp biomass past 1998 (figure 3.4 data points). Krill and salp abundance is thought to be strongly influenced by the SOI, the ACW (Antarctic Circumpolar Wave) which brings cold deep water the surface at the peninsula, and the placement of the sACCf (southern Antarctic Circumpolar Current Front) (Lee et al., 2010). Salp abundance has been shown to have a strong negative correlation to sea ice extent in the previous winter, which is negatively correlated to SOI (Loeb et al., 2009). SST was tested to fit the model as it is a contributing factor to both the ACW and sACCf, although there are many other important factors contributing to the dynamics of these environmental drivers. Sum of squares (SS) value for the SST fitted model was 68.57, and SS for the SOI fitted model was 78.95. With biomass trends for most species being similar (see appendix P for graphs of all functional groups), it was decided that the SST driver provided a better fit based on SS values.

Model Results

Estimates of all parameters in the Monte Carlo routine (figure 3.5 with CV values in table 3.2) from 1000 iterations were unable to improve SS value, however they did provide ranges of acceptable input parameter values. In general, the model was able to support a larger range of biomass for marine mammal species with higher initial biomasses (weddel seals, crabeater seals, fur seals, minke whales and humpback whales). Ranges for penguin groups were relatively low, although the model is able to support a much higher biomass of flying birds. Fish groups share the same CV value, with the general trend of biomass range proportional to starting value. *P. antarcticum* and *N. gibberifrons* have the largest starting biomasses and the largest range of acceptable biomasses, likely due to their importance to predators diets. Demersal fish (shallow and deep groups) and toothfish, show very narrow ranges of biomass. The largest biomass ranges for benthic invertebrates are for sponges and worms, which have the largest biomasses in surveys (Jazdzewski et al., 1986; Saiz-Salinas et al., 1998; Piepenburg et al., 2002).

3.4. Results

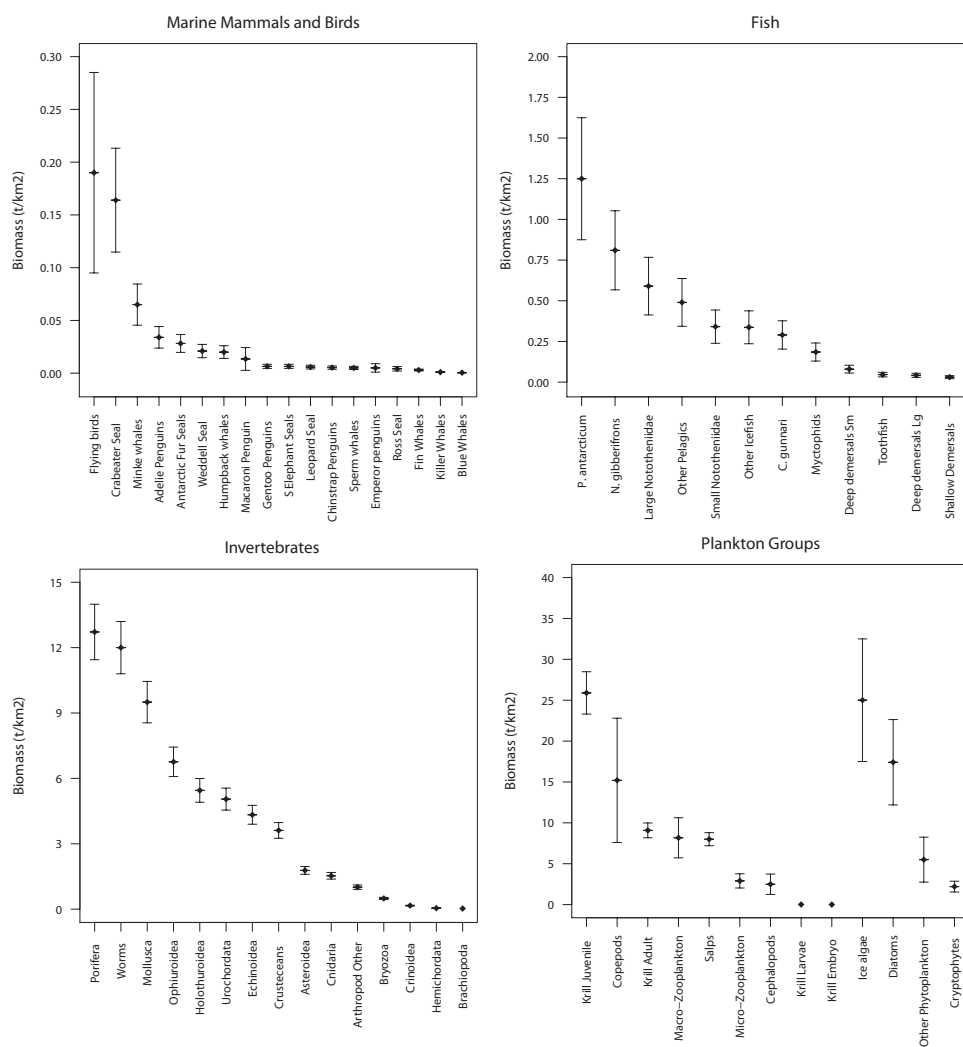


Figure 3.5: Monte Carlo estimates of biomass using CV values from table 3.2

3.4. Results

Copepods have the largest range of biomass for zooplankton groups, with juvenile krill and macro-zooplankton having the next largest ranges. Salps in comparison to other zooplankton have a narrow range of acceptable starting biomass indicating the model cannot support a large starting biomass of salps, although the fitted model indicates higher biomasses are supported throughout the last 30 years. Results suggest that the model can support higher biomasses of diatoms and ice algae, with lower biomasses of warmer water associated producers (cryptophytes and other producers).

The trophic level of catches (TL_C) declines from an initial value of 3.39 in 1978 to 2.34 in 2007. This is due to the catch being largely comprised of fish species in early years of the model (figure 3.2), as test fisheries operated in the early 1970s in the model area (CCAMLR, 2008b). This combined with low krill catches in early years resulted in a higher TL of catches than in later years where krill dominate, as krill are at a lower trophic level than fish species. Trophic level of the ecosystem (TL_E) maintains a relatively stable trend, hovering around a TL of two, denoting there is a large proportion of the ecosystem biomass at lower trophic levels. While ecosystem TL appears to indicate the ecosystem maintains stability, total biomass shows declines from $209\text{t}\cdot\text{km}^{-2}$ in 1978 (mean=206 from 1978-1982) to an ending value of $135\text{t}\cdot\text{km}^{-2}$ in 2007 (mean=159 from 2003-2007).

Table 3.3: Trophic level of the ecosystem TL_E and catches TL_C along with cumulative biomass of the ecosystem $\text{t}\cdot\text{km}^{-2}$ presented in 10 year increments throughout model simulation. Data presented are calculated from the SST fitted model.

Year	TLE	TLC	Biomass
1978	1.91	3.39	209.73
1988	2.07	2.30	186.59
1998	2.01	2.28	156.75
2007	1.98	2.34	134.97

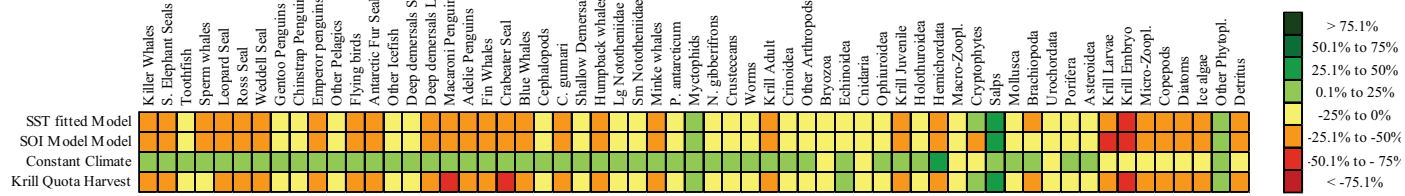


Figure 3.6: Simulation results for the fitted model and other scenarios. Values are presented as the percent (%) change in biomass from the starting (1978) value. Ending biomass is calculated as the mean from 2002-2007 to avoid exaggerations of biomass in lower trophic levels due to warm or cool years.

Constant Climate and Increased Harvest Scenarios

For hypothetical scenarios testing the model sensitivity to harvest levels and environmental drivers, the SST fitted model was used. Ending values were calculated as the 5 year average biomass from 2003-2007. Under the "Constant Climate" scenario, environmental trends (SST and ice cover) were repeated as monthly values for 1978, the first year of the simulation. While this retained seasonal patterns, the annual averages remained constant, and harvest patterns of the past remained intact. Total primary production still declines in this scenario, although less than 5%. Cryptophytes, diatoms, and ice algae all decline less than 10% due to top down effects, while the other primary production group increases less than 10%. Detritus decline is less than 3%. Although the biomass of detritus and primary production does decline even with constant climate, there is still enough biomass of these groups to result in increased biomass for the ecosystem, and most functional groups and the total ecosystem biomass. Total biomass of the ecosystem increased to $217.9t \cdot km^{-2}$, indicating that if environmental drivers (via primary production) remained constant, the ecosystem could support a total higher biomass than 1978 values.

All marine mammal groups increase with values ranging from 17.23% (weddel seals) to 6.52% (minke whales). Impacts to penguins and flying birds were all positive, with chinstrap penguins increasing the most at 20.37%, and emperor penguins at 11.85%. Fish groups increased from 12.26% (other pelagics) to 23.02% shallow demersals. Invertebrate groups show mixed results with urochordates, bryozoans, and cnidarians each decreasing near 5%, while the rest of the invertebrate groups (excluding zooplankton groups) increase up to 20.02% for holothuroideans. For zooplankton functional groups, copepods, micro-zooplankton, macro-zooplankton, krill embryo, and juvenile krill all declined with values ranging from 0.23% (krill larvae) to 10.63% (copepods). For zooplankton groups that increased, values ranged from 5.79% (juvenile krill) to 16.57% (salps). The total biomass of all krill groups combined increased by 6.42%.

For the "Increased Harvest" scenario, krill catches were forced at quota

levels to assess the impacts on the ecosystem if krill had been harvested at the quota maximum throughout the past. Environmental drivers with past trends of decreasing ice and increasing SST were used in this scenario. Results for this scenario are very similar to the past trends, indicating increasing harvest rates would not greatly alter the ecosystem structure. Differences between the increased harvest scenario and the SST fitted model were minimal; all functional groups showed less than $\pm 3\%$ difference in ending biomass between the models. Of the krill functional groups, adult krill had the largest difference declining a further 2.16% under the increased harvest scenario to show a total decline of 35.61%.

3.5 Discussion

Balancing of the Ecopath model indicated contributions of krill to the diets of predators was higher than the Ecopath model initial biomass of krill could support (see appendix J for diet descriptions). Possible explanations for this include overestimation of krill in the literature as a dietary component, higher biomass of krill than initial parameterization of the Ecopath model, or contributions of krill to predator diets from outside the model area. While diet studies are primarily based in the austral summer where there is greater access to the region, samples of predators stomach contents are likely to overestimate the importance of krill as they are more available during the spring and summer months.

Some studies have accounted for the diets of seals and penguins during the winter, establishing the importance of other non-krill prey items to predators diets, namely fish, cephalopods, and other zooplankton species (Green, 1986; Whitehouse and Viet, 1994; Reid, 1995; Kirkwood and Robertson, 1997; Lowry et al., 1998; Clausen and Putz, 2003). Studies suggest myctophids may be a key energy-rich dietary component for lactating fur seal and some stages of chinstrap penguins which may rival krill as an energy source in Antarctic ecosystems (Ichii et al., 2007; Flores et al., 2008). When only summer diets were available for species within the model, care

3.5. Discussion

was taken to include prey items for winter feeding, should this be an issue⁷. Yet, even with a substantial annual biomass of krill in the Ecopath model $37g \cdot m^{-2}$, diets of predators had to be altered from compositions suggested in the literature to be less heavily weighted on krill. This is perhaps due to a lack of understanding of winter diets and highlights the need for more winter based diet studies of krill predators. Additionally, it could be explained in the model through a higher growth rate (or an increased P/B ratio in the model). P/B values were taken from krill studied in the Cooperation and Cosmonaut Seas, which may be higher in the coastal areas of the Antarctic peninsula (Atkinson et al., 2008). Increasing the P/B value in the initial Ecopath model would allow for higher contributions to the diets of predators. It is also possible the total biomass of krill present in the ecosystem at the time of the Ecopath model was underestimated by Atkinson et al. (2004). With an increased biomass in the Ecopath model, it may be possible there would be enough krill available to support higher contributions to the diets of predators.

Of the Ecosim models the fitted model using SST was selected, as it provided a lower SS. Although the salp trend is not captured in more recent years (1998 onwards), recent evidence suggests there may have been a leveling out of salp abundance resulting in smaller fluctuations than the data suggests. Salp populations have been more consistently present in the shelf portion of the Antarctic Peninsula since 1999, with a strong negative correlation to the number of ice days in the previous year (Ross et al., 2008), lending credibility to the theory of salp populations leveling out after 1998 (Lee et al., 2010). The model fitted with SOI on producers provides a better fit to salps as it captures the more extreme fluctuations in later years (after 1998). However, the inclusion of the salp mediating function for the SST driven model lowers the SS value below that of the SOI driven model. While other drivers were tested (sea ice extent, air temperature and open water extent) there is the potential that better drivers exist. The movement of the Antarctic Circumpolar Wave (ACW) and the placement of the

⁷For example this is not an issue for baleen whales whom are only present in the summer months and feed almost exclusively on krill and other zooplankton.

southern Antarctic circumpolar current (ACC) front is believed to influence krill and salp abundance along with the SOI (Lee et al., 2010). The climatologies associated with krill and salp locations were not correlated (Ross et al., 2008), indicating environmental factors for each may not be mutually exclusive. While in other Antarctic areas spatial overlap of krill and salps is not common, at the peninsula the southern boundary of the ACC is relatively close to the shelf of the continent (Ducklow et al., 2007), promoting greater mixing and possibly pushing more suitable salp conditions closer to the peninsula. However, long-term, standardized datasets were not available for modeling purposes, but should be explored in the future.

Differences between the two model fits show changes to the ending composition of primary producers. However, total production biomass remains fairly constant. Cumulative biomass for all primary producer starting groups was $53.50\text{t}\cdot\text{km}^{-2}$ in 1978, with the ending value for SST fitted model at $32.01\text{t}\cdot\text{km}^{-2}$ and $31.34\text{t}\cdot\text{km}^{-2}$ for the SOI fitted model. The other phytoplankton group and cryptophytes show the largest changes between the two models with biomass demonstrating similar trends between the two models, and variance caused by the drivers affecting inter-annual variability (appendix P).

Overall the decrease in primary production of nearly 40% (for all producer group biomass combined) is much higher than the 10% decline estimated from Gregg et al. (2003). Although it should be noted that the decline of 10% is from satellite data and excludes the contribution of ice algae to total production (Gregg pers. comm), meaning the declines are based primarily on summer bloom values. Chl a concentrations from satellite models from 1975-2002 show general decreasing trends in the Atlantic sector of the Southern Ocean, with values at the Antarctic Peninsula declining by roughly 12% (Lee et al., 2010). Chl a concentrations from Elephant Island peaked during 1994-1996, showed low values from 1997-1998 and increased again in 1999-2000 and 2002 (Loeb et al., 2010). In the Antarctic ice algae from multi-year ice can contribute at least 20% to total production, with fast ice showing chl a concentrations up to $120\text{ mg chl a}\cdot\text{m}^{-2}$ (McMinn et al., 2000). It has been noted that phytoplankton is decreasing in the western Antarctic

3.5. Discussion

Peninsula (WAP) region and increasing in the southern WAP region due to wind stress and ice free conditions (Montes-Hugo et al., 2009). With ice algae being an important contributor to production, declines in sea ice (and therefore ice algae) are likely to be underestimated by satellite data, or samples only taken in the summer months.

The fitting process for krill fails to capture the high biomass in 1982, which could be due to a number of reasons. First, the time series data was only applied to the adult group and not the entirety of all krill functional groups. Looking at the biomass trends over time (appendix P), juvenile krill have a larger biomass and a slightly different trend over time⁸. Combination of these groups could provide a better fit to data. In addition sampling of zooplankton is highly variable, and could add to variability in data used to fit the model.

As long term timeseries are hard to come by, the ones used in the fitting chinstrap, gentoo, and Adelie penguins were obtained from the PALMER LTER research conducted on Anvers Island (Fraser, 2006). While the research indicates declines of Adelie penguins at Anvers Island are representative of larger scale changes in population, surveys from other breeding locations indicate mixed changes in chinstrap populations. Chinstrap penguin populations have been decreasing since 1981 at King George Island, while at Signy Island populations only started to decline in the 1990s (Woehler et al., 2001; Croxall et al., 2002). For Adelie penguins populations at Signy Island have shown to be stable in the 1970s with fluctuations in the 1980s and 1990s while penguins at Anvers Island have been identified to decline since the 1970s (Woehler et al., 2001; Croxall et al., 2002). In the past it was believed ice-dependent species such as Adelie penguins were decreasing and ice-avoiding species such as chinstrap and gentoo were increasing, but more recent data suggests all species are declining. The paradigm has shifted from the idea that penguin populations were driven by sea ice to

⁸It should be noted the same timeseries was applied to the juvenile krill group during the fitting process. Only a small portion of juvenile krill would be captured by sampling nets, and therefore be included in the trend. Addition of the krill timeseries to the juvenile krill group did not enhance the model fit.

3.5. Discussion

one that populations are dependent on krill, which is driving changes in the populations (Trivelpiece et al., 2010). Support for this stems from research highlighting declines in both Adelie and chinstrap populations at the South Shetland Islands up to 75%, with changes in krill biomass potentially explaining these trends (Trivelpiece et al., 2010). Within the model, declines in all penguin species are attributed to changes in krill. While there are no direct linkages to sea ice or other environmental factors in the model, declines of penguin biomass caused by changes in the food web range from 18% for chinstrap to 50% for macaroni penguins. If immigration rates are removed from the model to better represent large scale abundance trends for chinstrap and gentoo penguins, biomass declines a further 24% for chinstrap and 18% for gentoos. Maximum declines of roughly 50% for macaroni penguins are lower than the 75% declines in population noted in Trivelpiece et al. (2010). However, while model results are presented in biomass and other literature in number of breeding pairs, it is important to note that the model supports the theory that changes in krill are responsible for declines in penguin populations. Recent literature indicates immigration rates for chinstrap and gentoo penguins should be removed from the model (Trivelpiece et al., 2010).

Both fitted models indicate that changes in primary production and detritus are responsible for declines within the model, implying this is a bottom up ecosystem. The vulnerability for most predator prey interactions was set to the default of 2 indicating a mixed interaction (neither bottom-up or top-down), however changes in higher trophic level biomass are highly influenced by lower trophic level biomass demonstrating strong bottom up influences.

The trophic level of the ecosystem remains constant in the face of overall declines in biomass indicating even declines across trophic levels. As the past demonstrates boom and bust cycles of krill and salps (Brierley and Reid, 1999), there is the potential for a "leveling out" of these species in terms of biomass since the mid 1990s as suggested by Loeb et al. (2009) and Lee et al. (2010). For the constant climate scenario, an increase in most functional groups is observed along with a higher total biomass for the

3.5. Discussion

ecosystem. As climate drivers are kept constant, this simulation allows the opportunity to assess the potential of stability in lower trophic levels, rather than large annual fluctuations often observed in high latitude ecosystems. While the annual ice and SST patterns are repeated, there are no net changes in model drivers, allowing the changes that do occur in the model to be driven by trophic interactions and harvest. This is supported by Monte Carlo simulations on the Ecopath starting parameters (Figure 3.5), where higher initial biomass of species is supported.

Reflecting on the krill surplus hypothesis; the notion that as large baleen whales were harvested throughout the first half of the 20th century, there was a large availability of krill for other whales (minke), seals and penguins (Laws, 1977). While the model does not assess this issue on the same temporal scale, additional, more specific simulations would be required to address this issue fully. However, the model is able to support a higher total biomass, and higher biomasses of predators as shown through Monte Carlo simulations and the constant climate scenario. If commercial whaling reduced baleen whale populations enough to cause large scale increases in seals and penguins, it would have occurred before the start of the model, therefore declines should be considered in the context of recently inflated populations. It is possible that restructuring of some seal, penguin, and whale populations is occurring. Since ice and krill biomass has declined since this time, the "surplus" caused by whaling would have been short lived in the ecosystem, and would not be representative of present day populations. Krill predators would have had to reach maximum abundance pre 1970s, before ice declines were observed, and inputted Ecopath parameters would reflect changes that already occurred to krill predators in the ecosystem. However without some indication as to which populations are changing we cannot make these assumptions within the model, only to note total biomass declines.

The increased harvest scenario shows little change to the biomasses of functional groups or the total ecosystem, while alterations of climate drivers do identify large changes in the model. It is possible that the model is an artifact of the literature used to create it, as much of the research in the Southern Ocean is focused on bottom up approaches (Ainley et al.,

2007). While top down approaches to understanding the ecosystem have been employed, generally focusing on management of the ecosystem (Nicol et al., 2007), incorporation into the model does not cause the profound changes that bottom-up forces cause.

Harvest of krill at quota levels does not significantly alter ecosystem structure, denoting increase in harvest levels would be appropriate. However, one should take caution in this interpretation as the model only runs on a temporal scale rather than a spatial scale. CCAMLR quotas are set based on ecosystem management, but recent evidence indicates that spatial overlap between krill predators and fisheries is an important link in determining harvest levels. Marin and Delgado (2001) showed that roughly 80% of the krill catch was taken from within penguin foraging areas near the Antarctic Peninsula, suggesting fisheries are in direct competition with predators (Hewitt et al., 2002, 2004). The suggested implementation of Small Scale Management Units (SSMUs) will limit spatial harvest by breaking down quotas into smaller spatial scales to reduce competition with land based predators (Hewitt et al., 2004; Flores et al., 2011). In this respect the model is less sensitive to declines in krill, as all functional groups are assumed to be in a homogenous space. However in reality small scale declines in krill, or other prey items can cause declines in breeding success, or starvation as shown in the past (Reid and Arnould, 1996; Brierley and Reid, 1999).

Conclusions

Construction of an ecosystem model and past simulations indicates bottom-up interactions are important at the Antarctic Peninsula. Monte Carlo routines and past simulations at constant climate levels demonstrate the ability of the system to support a higher total biomass. Increasing the krill harvest to quota levels does not result in large changes in the ecosystem, when compared with the impacts of environmental changes. Although more detailed spatial analysis should be considered before management decisions are made.

Chapter 4

Future Impacts of Hunting, Fishing, and Climate Change on the Hudson Bay Marine Ecosystem

4.1 Synopsis

Using the ecosystem model constructed in chapter 2, simulations depicting harvest and changes in climate were extended into the future to assess the long term impacts on the Hudson Bay ecosystem. Numerous scenarios corresponding to IPCC climate scenarios were used, with future environmental trends extracted from global climate models and incorporated into the ecosystem model to continue past environmental drivers. In addition, different harvest levels were combined with each possible climate scenario assessing cumulative impacts on the ecosystem. Continuation of environmental drivers resulted in more pronounced shifts in the food web from an ice algae-benthos-benthic fish dominated pathway to a spring bloom-zooplankton-planktivorous fish dominated ecosystem. Bottom up changes in the food web are identified as important factors for determining changes in lower trophic level organisms such as benthos, zooplankton, and fish. Harvest of higher trophic levels is identified as a more important factor when compared to environmental changes. Simulations indicate some stocks are unable to sustain current harvest levels and may be extirpated (narwhal, eastern Hudson Bay beluga, polar bears, and walrus). Larger populations

of marine mammals (ringed seals and western Hudson Bay beluga) are identified to be able to withstand an increase in harvest and continue to increase even under a high climate scenario coupled with an increase in harvest rates. Management and conservation focused on marine mammals should be directed to prevent over-harvest of vulnerable populations, as this is indicated as a more severe threat in the model.

4.2 Introduction

High latitude marine ecosystems are particularly sensitive to climate change (ACIA, 2004) as small changes in temperature can have large effects on the extent and thickness of sea ice (Smetacek and Nicol, 2005), and can fundamentally alter the structure of the food web. The Canadian Arctic is already experiencing a reduction in sea ice thickness and a decrease in sea ice extent (Holland et al., 2006; Arrigo and Pabi, 2008). In addition, while the reliance on hunting has decreased it is not expected to disappear (Csonka and Schweitzer, 2004), especially since human populations are still increasing even though growth rates have slowed since peaking in the 1960s (Bogoyavlenskiy and Siggner, 2004). These stressors (hunting and climate change) have been shown to cause changes to the Hudson Bay ecosystem such as declines in polar bear populations (Stirling et al., 1999, 2004). Here we aim to explore the potential changes to come under increased environmental and hunting pressure, not only to the species they impact, but how these changes will affect the marine ecosystem structure and the cumulative effects of these impacts.

Temperatures for Hudson Bay have shown increases ranging from 0.5-1.5°C from 1955-2005 (Hansen et al., 2006a), and warmer temperatures have been shown to alter the mean ice freeze-up and break-up dates by 0.8-1.6 weeks in spring and fall (Hochheim et al., 2010). Also, from 1978 to 1996 declines in sea ice area from $2000 \pm 900 \text{ km}^{-2} \text{ y}^{-1}$ have been observed (Parkinson et al., 1999). Ice plays an important role in the ecosystem, not only as a platform for marine mammals to hunt and breed upon (seals, polar bears) but also as an important regulator of ice algae, a food source

for lower trophic levels through the winter and into the spring. Algae frozen within the ice are released from brine channels during ice growth and melting (Melnikov, 1998), and exported to the water column. During ice melt, this release combined with low zooplankton biomass (and therefore low grazing rates) in the early spring leads to a higher export to the benthos (Lavoie et al., 2009), this effect is magnified when annual melting of ice is shifted earlier (Hunt et al., 2002). In relation to total production, the contribution of ice algae in southeast Hudson Bay has been estimated at 25% (Legendre et al., 1996), and ranges from 3-57% for other Arctic and sub-Arctic areas (Gosselin et al., 1997).

As annual ice levels decline less ice algae is exported to the benthos, potentially decreasing benthic biomass and the fish and invertebrates reliant on these benthic food sources. This is proposed to favor a phytoplankton-zooplankton dominated system over the ice algae-benthos ecosystem typical of the Arctic (Piepenburg, 2005). In addition, lengthening of the growing season and increases in temperature are expected to cause increases to the spring/summer bloom. In the Beaufort Sea, future climate change is anticipated to extend the summer phytoplankton bloom which favors zooplankton development, mainly copepods in the region (Lavoie et al., 2010). This will likely enhance pelagic feeding animals in the food web. Studies on bird diet show shifts from benthic feeding fish to pelagic based species indicating a change in the ecosystem (Gaston et al., 2003).

Currently, marine mammals found within the Hudson Bay (HB) region are hunted and consumed through subsistence hunts. However declines in some populations, e.g. eastern HB belugas (Hammill, 2001; DFO, 2002a; Gosselin et al., 2002; Gosselin, 2005; Hammill et al., 2009), northern HB narwhal (COSEWIC, 2004a), and polar bears (Lunn et al., 2002; Stirling and Parkinson, 2006) may jeopardize the ability for hunting to continue at present levels. For marine mammal stocks not demonstrating declines, alterations to the food web caused by changes in climate may ultimately affect population levels, although thresholds have not been identified (see chapter 2).

The human population in the Nunavut portion of Hudson Bay has more

than doubled from 1981-2006, increasing from nearly 4700 to 9500 inhabitants (Statistics Canada, 2006). While growth rates are projected to decline, estimates remain positive indicating continued future growth. Future projections for all communities in Nunavut suggest continued increase for the territory from 32,000 to 45,000 individuals from 2009 to 2036, with growth rates slowing to 1.1% per year toward the end of the projections (Nunavut Bureau of Statistics, 2010). While these predictions assume a decline in human growth rates, many communities are still showing large increases. Compounding the reliance on harvested foods is the belief that the prices of store bought foods will continue to increase despite subsidy programs offered to northern residents (Windeyer, 2011b,a). Food price increases coupled with rising populations may intensify the demands for country foods (foods hunted or gathered from the land).

Using an existing food web ecosystem model from 1970-2009 (chapter 2), driven with environmental variables (sea surface temperature (SST) and sea ice) and catches of various species, future simulation emulating different levels of climate change and harvest are utilized to assess the impacts to the food web. While producer groups were driven in the model using SST and sea ice, these showed the greatest responses to environmental changes over time, accounting for changes in the food web. Loss of Arctic sea ice due to increases in temperatures is believed to increase productivity up to three times the 1998-2002 production levels (Arrigo and Pabi, 2008). In addition, less sea ice will increase the availability of light to phytoplankton, a limiting factor of production in some Arctic ecosystems (Conlan et al., 2008). These impacts can account for alterations to the fish communities, through disruption of benthic-pelagic coupling. As sea ice declines, so does the amount of algae exported to the benthos, thus causing declines in benthic and benthic feeding fish species. Declines to polar bears, narwhal, bearded seals, and the eastern Hudson Bay stock of belugas were attributed to hunting pressure. In order to test the Hudson Bay ecosystem model's sensitivity to further impacts of hunting and climate change, past model environmental and harvest drivers were continued into the future under a variety of hunting and climate change scenarios.

4.3 Methods

Modeling Approach

For the mass balancing model approach the Ecopath with Ecosim (EwE) software was used, as it utilizes information on trophic interactions to identify changes to the ecosystem (Christensen and Pauly, 1992; Walters et al., 2000; Christensen and Walters, 2004) and provides a common framework between systems studies by different researchers (Plaganyi and Butterworth, 2004). It is currently used in over 154 countries with more than 6000 users, and has been named one of NOAA's top 10 breakthroughs (NOAA, 2006). While single species models can offer greater details for factors affecting individual species, they fail to capture the linkages important for assessing a food web (Fulton and Smith, 2004). In addition, it would take numerous single species models to identify the potential impacts of the ecosystem that can be addressed with one ecosystem model (Fulton and Smith, 2004).

Model Structure

Future simulations are based upon an existing ecosystem model created for the Hudson Bay marine ecosystem (chapter 2). The existing model was fitted using catch data from 1970-2009 for all harvested species in the region in addition to SST and ice cover as environmental drivers to the ecosystem. In the past fitted model, SST and sea ice were used as environmental drivers with data extracted from the global Hadley Centre Sea Ice and Sea Surface Temperature model (HadISST) from the British Atmospheric Data Centre (BADC, 2010) and used as drivers for primary producer species groups. The geographical region of the model includes James Bay along with Hudson Bay, but excludes Hudson Strait and Foxe Basin (see chapter 2, figure 2.1).

The model contains two producer groups; ice algae and pelagic production. The sea ice was inputted as percent ice cover to the region as a driver for the ice algae producer group, while SST was used as a driver for pelagic producer. Ice algae was driven with percentage ice cover rather than ice thickness, due to Chl *a* biomass in ice cores being found in the bottom 4 cm

4.3. Methods

(Juul-Pederson et al., 2008). Furthermore, SST and open water (as calculated by areas not covered by sea ice) have been used in Arctic wide models to predict future production changes (Pabi et al., 2008). The pelagic production group was thus driven with SST to mimic the seasonal production peak in the summer.

Temporal simulations were created using equation 4.1, where dB_i/dt represents the change in biomass (B) for group i over the time interval t , with starting biomass B_i . g_i represents the net growth efficiency (production/consumption ratio), the $\sum_j Q_{ji}$ is the total consumption on group i , and $\sum_j Q_{ij}$ is the predation of all predators on group i . MO_i represents the other mortality term (for mortality associated with old age), F_i is the fishing mortality rate, I_i is the immigration rate, e_i is the emigration rate, with the combined term $B_i \cdot (e_i - I_i)$ as the net migration rate. Mortality referred to within the paper entails predation and harvest mortality unless specifically identified.

$$dB_i/dt = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (MO_i + F_i + e_i)B_i \quad (4.1)$$

Using the trophic level of individual species groups (equation 4.2), mean ecosystem and catch trophic levels, TL_E and TL_C , were calculated for each scenario (using equations 4.3 and 4.4) and presented as the average over the last ten years of each simulation.

$$TL_i = 1 + \sum (X_a * TL_a) + (X_b * TL_b) + (X_c * TL_c) \dots \quad (4.2)$$

$$TL_E = \sum \frac{B_i}{B_E} * TL_i \quad (4.3)$$

$$TL_C = \sum \frac{C_i}{C_E} * TL_i \quad (4.4)$$

The Trophic level TL of each group was calculated with EwE, where primary producers have a TL of 1, primary consumers with 100% of their diet as producers have a TL of 2, and consumer TL is calculated based on the diets of

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other organisms (Christensen et al., 2007). For consumers TL of each group is calculated based on the TL of prey groups (a,b,c,etc.), TL_a, TL_b, TL_c , and the percent contribution of each prey group to the diet, X_a, X_b, X_c . B_i and C_i are the biomass and catch for group i , and B_E and C_E are the biomass and catch of the entire ecosystem, with values represented in $t \cdot km^{-2}$.

Scenarios

Table 4.1: Simulations of varying levels of climate and hunting. Scenario names indicate levels of hunting and climate. First letter indicates either a low (L) or high (H) climate scenario followed by the variance applied to the climate data (either past variance (1) or double the past variance (2)). The second letter indicates the level of hunting applied to the simulation; H1 for constant hunting at the 2009 levels, or H2 for double the hunting of the 2009 levels.

Climate Scenario	Hunting Scenario	Scenario Abbreviation
Low	Constant	L1H1
Low	Double	L1H2
Low double variance	Constant	L2H1
Low double variance	Double	L2H2
High	Constant	H1H1
High	Double	H1H2
High double variance	Constant	H2H1
High double variance	Double	H2H2

Future scenarios of climate change were created to identify plausible changes to the ecosystem. Data from the GFDL (Geophysical Fluid Dynamics Laboratory) CM2.1 coupled climate models (GFDL, 2010) were used as environmental drivers, in keeping with drivers used to fit the past model (chapter 2). Two main scenarios depicting a future "Low" and "High" climate scenario were created by extracting regional sea ice (percent cover) and SST data from the global model. The "Low" climate scenario corresponds to the IPCC (Intergovernmental Panel on Climate Change) constant 2000 scenario, while the "High" scenario corresponds to the A1B scenario⁹.

⁹The constant 2000 scenario assumes constant CO_2 emission equivalent to emissions for the year 2000. The A1B scenario, while considered a moderate emissions scenario, demon-

Each model simulation combined past and future datasets to provide a continuous 100 year time series. The past, re-created model (chapter 2) was combined with future climate drivers and harvest to assess the future impacts, with drivers being combined into continuous time series. For each future climate scenario (Low and High) spanning 2009-2069, 100 datasets were generated from the IPCC future climate models with difference variance levels, to test the model sensitivity to different climate and variance levels. Although no significant trends in variance were identified within the past data (1970-2009), we utilize different levels of variance for future data to test the impacts. Multivariate covariance with a normal distribution derived from the 1970-2009 environmental data (ice and SST) was applied to each of the future scenario datasets to generate 100 different time series datasets to force the Ecosim model. Each generated time series used the future data as the mean for the trend, and applied covariance from the past environmental data to generate a unique time series dataset to be used as a model driver. Next, a second set of environmental data was generated with a doubling of the variance in order to account for larger fluctuations in future climate variables. For climate scenarios L and H reflect a low or high climate scenario, while numbers 1 or 2 indicate whether normal or double variance was applied. Each dataset containing 100 simulations was used to drive the ecosystem model, with results recorded as the biomass of each functional group over the last 10 years of the simulation. Environmental drivers were extracted from the GDFL CM2.1 coupled model. Figure 4.1 identifies changes in ice cover and SST from the starting of the model in 1970 (using the HadISST model data for past data). The Low and High future climate scenarios demonstrate a lengthening of the ice free season, as well as increased temperatures and lengthening of warmer water periods (above 0°C).

strated higher sea surface temperature and lower ice cover than more extreme emissions scenarios such as the A2 scenario. Since the data displayed more extreme changes, it was chosen as more representative of a high climate change scenario

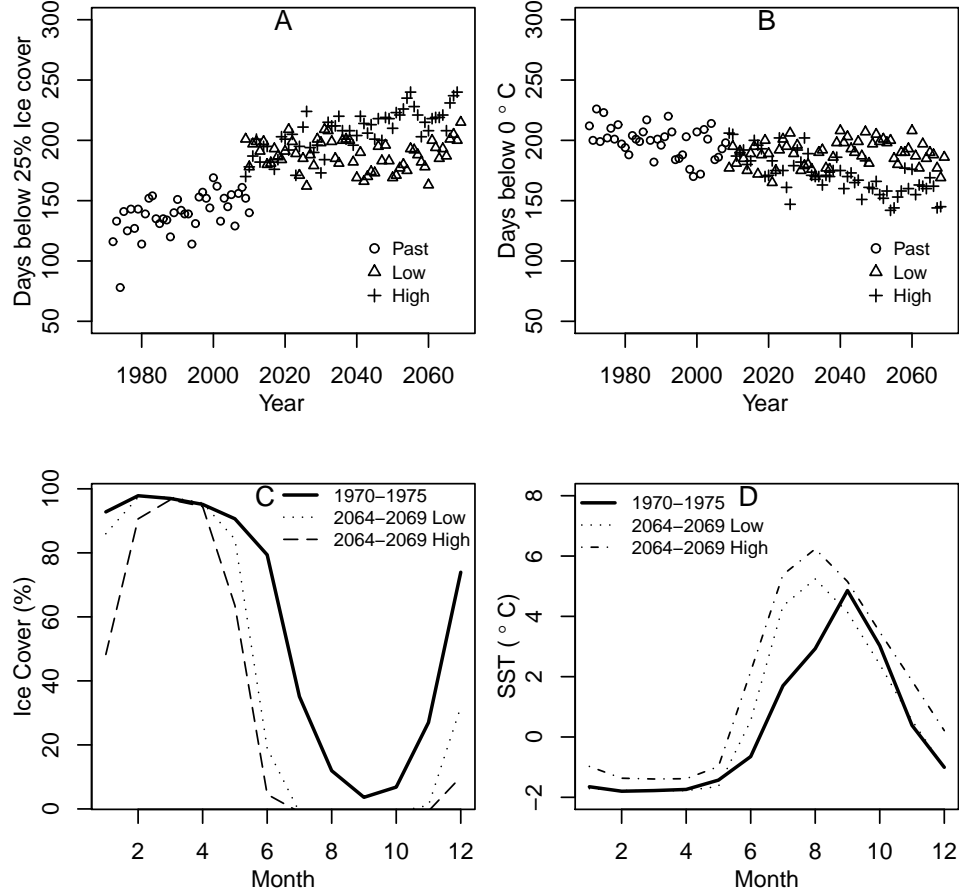


Figure 4.1: Environmental data used in model simulations. Past values were obtained from the HadISST data set while future data were extracted from the GDFL CM 2.1 coupled model. A and B compare number of days below 25% ice cover or days below 0°C for SST from the past with low and high climate scenario data. C and D show the ice cover and SST trends for the first 5 years of the model (1970-1975) compared with ending values (2064-2069) for the low and high climate scenarios.

Table 4.2: Summary of harvest values and hunting/fishing mortalities used for the initial Ecopath model (1970), and future hunting scenarios: H1 where catch and effort are constant to 2009 values, and H2 where catches and effort are doubled from the 2009 values.

Species Group	M (y^{-1})		Catch (#)			Reference
	1970	2009	1970	H1	H2	
WHB Polar Bears	0.033	0.078	44	47	94	Lee and Taylor (1994); Aars et al. (2005)
SHB Polar Bears	0.058	0.089	68	25	50	Lee and Taylor (1994); Aars et al. (2005)
FB Polar Bears *	0.024	0.026	142	106	212	Lee and Taylor (1994); Aars et al. (2005)
Killer Whales	0.051	0.040	0.25	0.738	1.477	Higdon (2007)(Ferguson pers. comm.)
Narwhal	0.008	0.072	23	82	164	DFO (1990, 1991, 1992, 1993, 1994, 1995, 1996, 1997, 1998); Stewart and Lockhart (2005); JCNB/NAMMCO (2009)
Bowhead	0.003	0.001	0.25	0.37	0.74	Higdon (2008)(Ferguson pers. comm.)
Walrus N	0.031	0.012	74	38	76	Strong (1989); NAMMCO (2005b); Stewart and Lockhart (2005)
Walrus S	0.009	0.019	8	14	28	Strong (1989); NAMMCO (2005b); Stewart and Lockhart (2005)
Beluga E	0.032	0.035	83	47	94	de March and Postma (2003); JCNB/NAMMCO (2009)
Beluga W	0.005	0.002	152	106	212	de March and Postma (2003); JCNB/NAMMCO (2009)
Beluga James	0.019	0.009	35	34	68	de March and Postma (2003); JCNB/NAMMCO (2009)
Bearded Seal	0.045	0.164	556	1187	2374	Stewart and Lockhart (2005); Statistics Canada (2006)
Harbour Seal	0.002	0.007	27	151	302	Stewart and Lockhart (2005); Statistics Canada (2006)
Ringed Seal	0.008	0.030	8436	45215	90430	Stewart and Lockhart (2005); Statistics Canada (2006)
Harp seal	0.014	0.051	91	576	1152	Stewart and Lockhart (2005); Statistics Canada (2006)
Birds	0.005	0.023	213703	1299831	2599662	Stewart and Lockhart (2005); Statistics Canada (2006)

Continued on Next Page

Table 4.2 Continued

Species Group	Fishing Mortality y^{-1}		Catch (tonnes)			Reference
	1970	2009	1970	H1	H2	
Arctic Char	0.0011	0.0051	421.4	2192.7	4385.4	Stewart and Lockhart (2005); Booth and Watts (2007); Statistics Canada (2006)
Atlantic Salmon	0.0002	0.0008	24.08	135.5	271.0	Stewart and Lockhart (2005); Booth and Watts (2007); Statistics Canada (2006)
Gadiformes	0.0003	0.0014	240.8	596.2	1192.5	Stewart and Lockhart (2005); Booth and Watts (2007); Statistics Canada (2006)
Sculpins/ Zoarcids	0.0007	0.0032	240.8	668.2	1336.4	Stewart and Lockhart (2005); Booth and Watts (2007); Statistics Canada (2006)
Capelin	0.0003	0.0012	120.4	884.1	1768.2	Stewart and Lockhart (2005); Booth and Watts (2007); Statistics Canada (2006)
Sandlance	0.0001	0.0004	60.2	507.0	1013.9	Stewart and Lockhart (2005); Booth and Watts (2007); Statistics Canada (2006)
Other Marine Fish	0.0002	0.0008	60.2	413.8	827.5	Stewart and Lockhart (2005); Booth and Watts (2007); Statistics Canada (2006)
Brackish Fish	0.0005	0.0022	24.08	132.7	265.5	Stewart and Lockhart (2005); Booth and Watts (2007); Statistics Canada (2006)
* Indicates hunting mortality is calculated based on a percentage of catches taking place within the model area.						

Under each of the various climate scenarios two hunting levels were tested: "H1": where catches and effort are kept constant to current (2009) levels, and "H2": where catches and effort are doubled from the 2009 values to reflect increases in human populations and the potential desire for higher catches (table 4.2). A summary of all model simulation combinations are provided in table 4.1.

Harvest data was provided from a variety of sources. For species hunted under regulations or quotas (polar bears, narwhal, belugas, walrus) recorded data was available for most years, or averages over time spans (generally 5 years) indicating averaged harvest rates. For unregulated species (birds, seals, and fish) catches were determined based on per capita rates from past harvest studies (Stewart and Lockhart, 2005), and driven with changes in human population levels based on past census data ¹⁰ (Statistics Canada, 2006). 100 simulations were run for each scenario. The average biomass ($t \cdot km^{-2}$) over the last 10 years of the simulation was used to get the mean and 95% CI for biomass changes of each functional group at the end of the simulation. This is mostly important for lower trophic level groups where the model is driven, and variations in the annual cycle of environmental drivers may cause changes in biomass.

4.4 Results

General Results

With the reductions in ice algae driven by sea ice there is a continued decrease in the availability of ice detritus to benthos. While this has already been identified through a past simulation from 1970-2009 (see chapter 2), longer simulations enhance this decline. Conversely, increased temperature favored the pelagic production to zooplankton pathway, causing a more pronounced shift from a benthic to a pelagic ecosystem (figure 4.2).

¹⁰It should be noted that for each functional group either catches or effort was applied, not both.

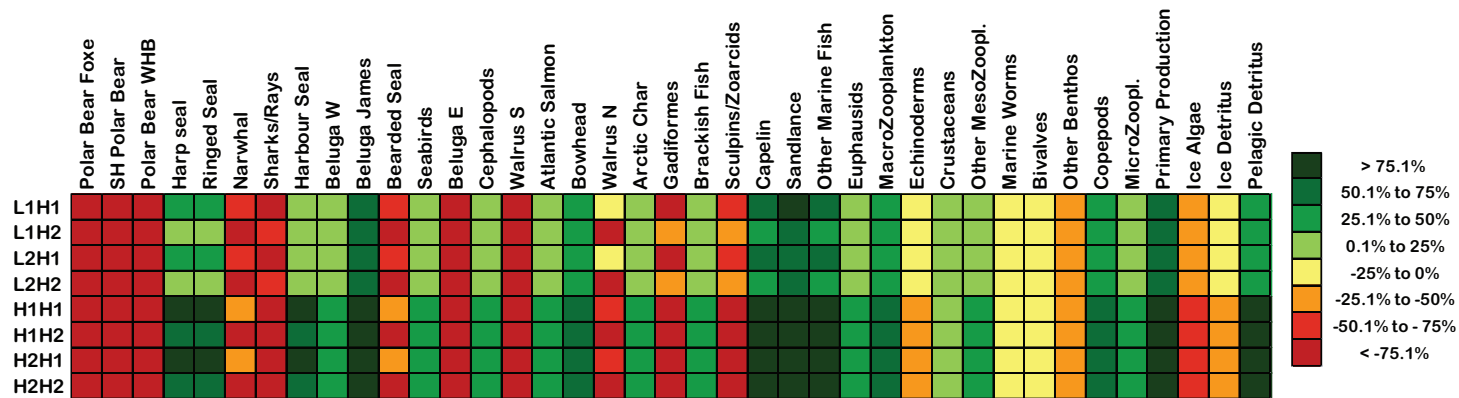


Figure 4.2: Changes in biomass for each scenario. Mean values of the 100 simulations are presented as the percent change from the starting 1970 biomass. Mean and 95% CI ranges of biomass for all simulations are presented in Figures 4.9, 4.10, 4.11, and 4.12. Killer whales were excluded from this figure as the biomass for this group was forced.

4.4. Results

Larger CI are observed for both biomass and mortality under scenarios with a doubling of environmental driver variance (figures 4.9, 4.10, 4.11 and 4.12), however mean values are not statistically different. This suggest the model is more sensitive to the general trend in climate drivers. Doubling harvest catch/effort identifies many species that can withstand increased harvest levels; most fish groups, harp seals, ringed seals, harbour seals, and beluga (western and James Bay stocks). Narwhal and walrus (north and south) were identified to have relatively stable changes in biomass for past simulations, however continued hunting at current rates is not sustainable. Polar bears have shown declines in the past model, and under continued constant hunting pressure these populations are extirpated.

Trophic level of the ecosystem continues to remain relatively stable for all scenarios with only small changes from the past (1970 values), low climate scenario, and high climate scenario. The trophic level of catch (TL_C) changes between scenarios as catch or effort was doubled, which resulted in similar proportions of each species being harvested, thus not greatly changing the composition of TL of catches (table 4.3). For 1970 the TL_C was 3.57. Under the low hunting (H1) scenarios this value increases to 3.62-3.65 reflecting small increases in catches of higher trophic level organisms. Under the high hunting scenarios (H2) the TL_C decreases slightly to 3.59-3.64. While it is important to note catches and effort were forced within the model, the slightly lower value under the high hunting scenarios is a result of declines in some populations (walrus, eastern beluga, and narwhal).

Trophic level of the ecosystem TL_E decreases from the 1970 value of 2.15 to a value of 2.11 for the low climate scenarios (L1 and L2), and starts to increase under the high climate scenarios (H1 and H2) to 2.13. While there is a loss of some higher trophic level predators (polar bears, narwhal, eastern HB beluga, and walrus), growth in other populations compensates for these losses with the other high trophic level animals (killer whales, western HB belugas, James Bay belugas, ringed seals, harp seals, and harbour seal). Total ecosystem biomass is higher under the future high climate scenario when compared to the 1970 value (table 4.3) indicating that although there is a loss of some species, the ecosystem is overall able to withstand a higher

total biomass.

Simulation results for key species are presented comparing the L1H1 scenario and the H1H2 scenario. As variance does not significantly change the mean biomass or mortality we examine the changes caused to these groups between these two most extreme scenarios.

Table 4.3: Trophic level of ecosystem (TL_E) and catches(TL_C) for the Eco-path model (1970) and each simulation. Results presented are averages values for the last 10 years of each simulation. Total biomass and total catch are presented in $t \cdot km^{-2}$ for all species within the ecosystem.

	TL_E	TL_C	Total Biomass	Total Catch
1970	2.155	3.578	58.305	0.002
L1H1	2.114	3.626	64.185	0.009
L1H2	2.119	3.594	63.511	0.018
L2H1	2.114	3.626	63.066	0.009
L2H2	2.118	3.593	63.095	0.018
H1H1	2.133	3.654	70.936	0.011
H1H2	2.135	3.638	70.640	0.020
H2H1	2.132	3.655	70.363	0.011
H2H2	2.134	3.638	70.801	0.020

Producers

Primary producers were directly affected by environmental drivers, as SST and ice cover were used as multipliers of pelagic production and ice algae, respectively. General trends show an average increase in biomass of 56% for pelagic production for the L1 (Low climate scenarios), and an average increase of 105% for the H1 (High climate scenarios) based on the 1970 value (figure 4.9). For ice algae the L1 scenario caused an average decrease of 31% and the H1 scenario caused a decrease of 53%. Increased flow from pelagic production to pelagic detritus resulted in an increase in pelagic detritus of 44% and 86%. The declines in ice algae result in decreases in ice detritus of 22% and 39% for the L1 and H1 scenarios respectively.

Biomass trends by scenario indicate mean biomass remains constant for the low and high climate scenarios, yet scenarios with high variance in model

drivers (L2 and H2), result in a larger variance in producer biomass at the end of the model simulation (figure 4.10). The composition of annual primary production was 70% pelagic production and 30% ice algae at the start of the model (1970). At the end of the Low future scenario pelagic production represented 84% of the annual primary production and ice algae represented 16% of annual production. Under the High climate scenario, pelagic production and ice algae contribute 91% and 9% to the annual production respectively. The total production (ice algae and pelagic production combined) increases by 15% and 18% for the Low and High climate scenarios.

Benthos

Benthic groups in the model decline due to decreased ice detritus from ice algae. The exception is the functional group crustaceans which includes benthic and pelagic crustaceans (Amphipoda, Cirripedia, Cumacea, Decapoda, Isopoda, Nebaliacea, Ostracoda, Pycnogonida, and Tanaidacea). For the other benthic groups, decreases are identified to range from 10% for bivalves to 26% for the other benthos group under the low climate scenarios, while these declines increase to 14% for bivalves and 42% for the other benthos group under the high climate scenarios. Benthic groups follow the same patterns as producers for ending biomass, i.e., low and high climate scenarios dictate the mean biomass, while higher variance in the environmental drivers is important in determining the variance in biomass results (figure 4.10). It is also important to note that while mean biomass of benthic groups is decreasing from the low to high climate scenarios, mortality rates are showing slight declines (figure 4.12) indicating changes in these groups are not caused by predators, but rather by bottom up forcing.

Zooplankton

While benthic groups generally mimic biomass and mortality patterns for ice algae, zooplankton follow the responses of pelagic production. Mean biomass increases from the low to high climate scenarios, with patterns in variance

replicating the patterns from the pelagic production group for each scenario (figure 4.10). Increases range from 18% for both the euphausiids and micro-zooplankton groups to 29% for the macro-zooplankton group under the low scenarios to 40% for euphausiids and 69% for macro-zooplankton under the high scenarios. Mortality rates do increase for zooplankton groups indicating higher predation through the food web. Increases in mortality are caused by increases in predators along with predators consuming more zooplankton to compensate for declines in benthic populations. As biomass increases with mortality rates (figure 4.12), it appears zooplankton are able to sustain higher predation levels, as the bottom up changes in the food web are able to support higher biomasses and thus the increased predation.

Fish

The fish trophic level of the ecosystem is where we start to identify the impacts of harvest in addition to prey changes. Fish groups are harder to distinguish as they are impacted directly through fishing, bottom up changes, and changes in predator population. In order to tease out some of these individual impacts, sandlance, capelin, and gadiformes are displayed in further details (figures 4.9 and 4.10).

Sandlance

Comparing the L1H1 and H1H2 scenarios for sandlance illustrates the increases in prey biomass between scenarios for the four highest ranked prey groups (copepods, euphausiids, other meso-zooplankton, and micro-zooplankton). Ringed seals had the largest contribution to total mortality as predation from this group alone for the initial 1970 value was $0.343y^{-1}$ out of a total mortality of $0.849y^{-1}$ (figure 4.3). Yet, as ringed seals increase in biomass from 29% to 64% for the L1H1 and H1H2 scenarios respectively, mortality caused by ringed seals only increases by 7% and 11% indicating the sandlance population is able to increase enough to meet predator's demands. Increases in hunting show catches increasing 6 to 20 times the starting values for the low and high hunting scenarios, with fishing mortality reaching

nearly 8 times the initial value. However total mortality (predation and fishing combined) is still lower than the 1970 value, even for the H1H2 scenario. While these values appear to be extreme, it should be noted that initial model values for fishing represented a very small contribution to total mortality, so even if these increases seem large, the fishing mortality for the H1H2 scenario was only roughly 1% of total mortality.

Capelin

Results for capelin are very similar to sandlance. The top four contributors to diet (copepods, euphausiids, macro-zooplankton and pelagic producers) all increase under the low and high climate scenarios. For the L1H1 scenario euphausiids have the smallest increase in biomass at 18%, while pelagic producers increase 57% (figure 4.4). For the high climate scenario euphausiids increase 40% and pelagic producers 105%. Predation by ringed seals and seabirds in addition to catches all increase from the L1H1 scenario to the H1H2 scenario, although total mortality is lower under both scenarios indicating capelin population are able to increase enough to meet these demands as capelin biomass more than doubles under the H1H2 scenario.

Gadiformes

The gadiform group representing Arctic and polar cods has a diet more heavily reliant on epibenthic prey items. Decreases in biomass of prey items forming the greatest contribution to the diets range from a 3% decline for echinoderms to a 27% decline for the other benthos group under the L1H1 scenario. Under the H1H2 scenario biomass declines of prey items continue ranging from 14% for bivalves to 42% for the other benthos group (Fig 4.5). Total mortality increases under both scenarios to a maximum of $0.549y^{-1}$ in the H1H2 scenario compared to the 1970 value of $0.477y^{-1}$. Although catches and fishing mortality have increased from past values, even under the High harvest scenario (H1H2) fishing mortality accounts for less than 1% of total mortality. Nearly all mortality is caused by predation, further supported by the increase in biomass of gadiformes under the high hunting

4.4. *Results*

scenarios. When predators are harvested in higher quantities, less predation prevents such large declines. This coupled with decreases in prey biomass identifies this group as declining due to both bottom up and top down forces.

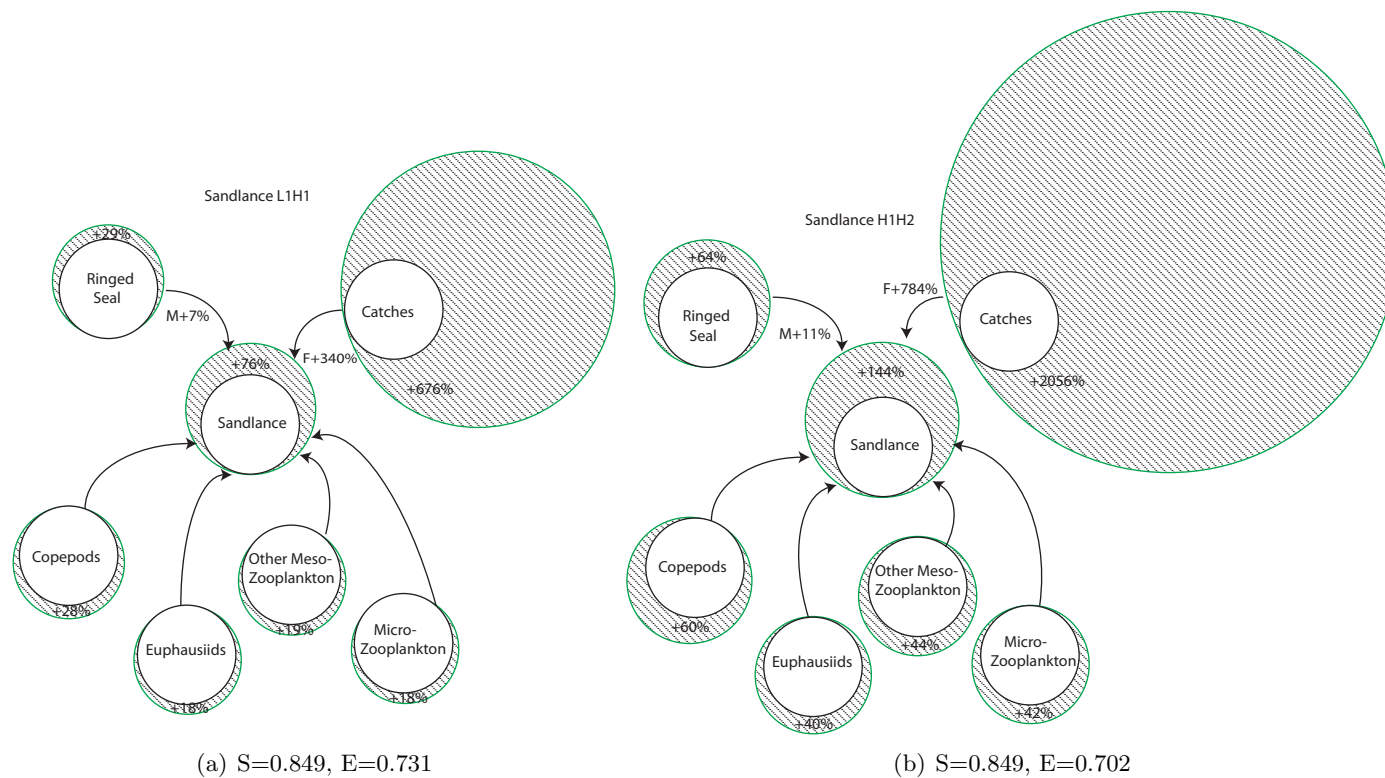


Figure 4.3: Changes in biomass for sandlance with important contributors to diet and mortality. S (mortality at the start of the model 1970) is presented along with E (mortality at the end of the scenario simulation). Ending values for biomass, mortality, and catches are averaged over the last 10 years of the simulation. Open circles represent initial biomass for the Ecopath model (1970 value), while the shaded circles represent the ending biomass and are scaled to represent the percent change in biomass.

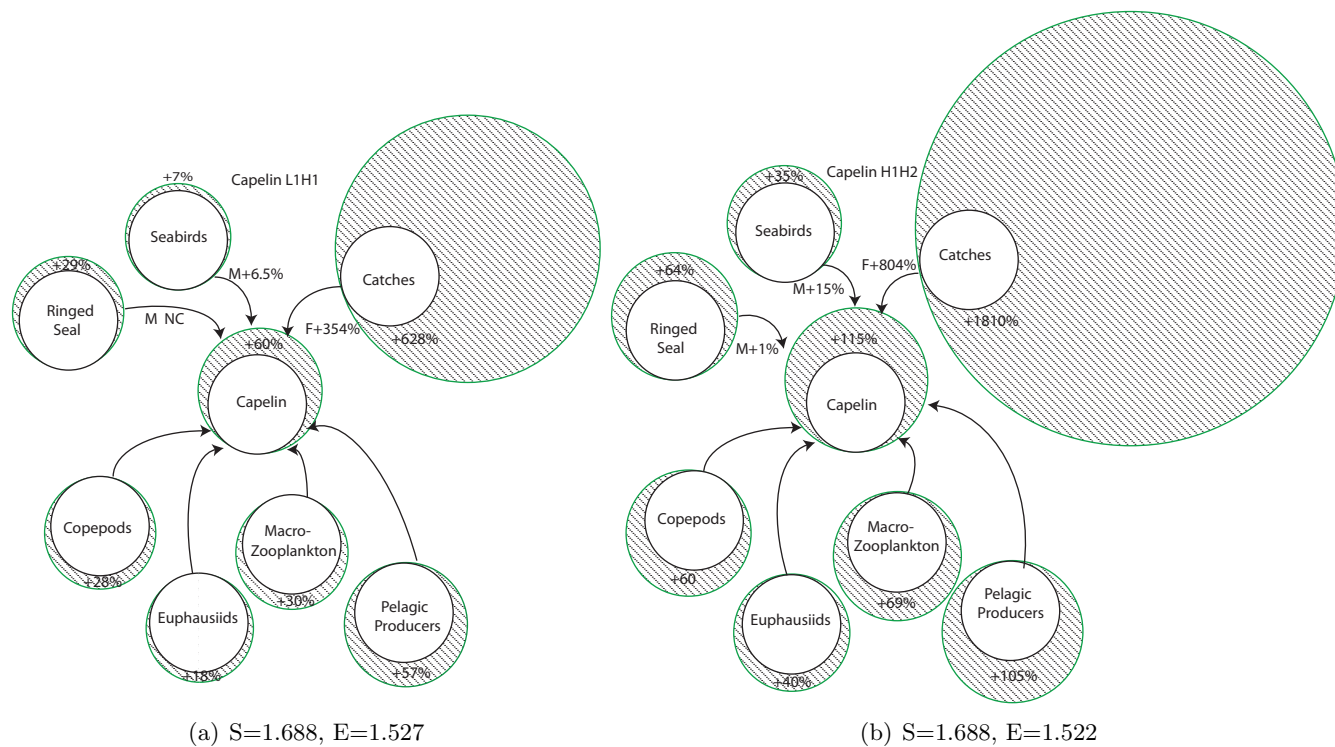
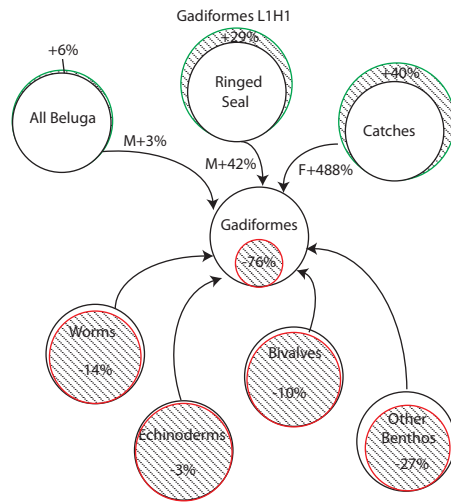
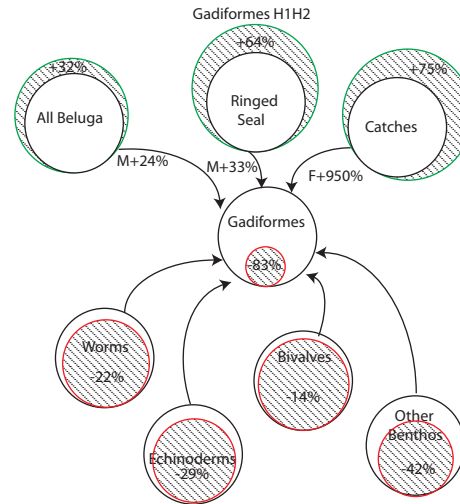


Figure 4.4: Changes in biomass for capelin with important contributors to diet and mortality. S (mortality at the start of the model 1970) is presented along with E (mortality at the end of the scenario simulation). Ending values for biomass, mortality, and catches are averaged over the last 10 years of the simulation. Open circles represent initial biomass for the Ecopath model (1970 value), while the shaded circles represent the ending biomass and are scaled to represent the percent change in biomass.



(a) $S=0.477$, $E=0.537$



(b) $S=0.477$, $E=0.549$

Figure 4.5: Changes in biomass for gadiformes with important contributors to diet and mortality. S (mortality at the start of the model 1970) is presented along with E (mortality at the end of the scenario simulation). Ending values for biomass, mortality, and catches are averaged over the last 10 years of the simulation. Open circles represent initial biomass for the Ecopath model (1970 value), while the shaded circles represent the ending biomass and are scaled to represent the percent change in biomass.

Other Fish

The biomass of the shark/ray group was very small in the initial 1970 model with the only predator being killer whales (0.5% of the total diet) with no fishing mortality. However as killer whales increased, the increased predation mortality was great enough to cause declines in the shark/ray model group. Biomass increased for the brackish fish group, Atlantic salmon, and Arctic char through bottom up changes as the diets contain large proportions of zooplankton or zooplankton feeding fish. While there are benthic components to some diets, they are small in comparison to the plankton contribution, and these groups have the ability to compensate for loss of benthic prey sources with plankton within the model. Mortality for these groups either declines or remains stable (figures 4.11 and 4.12) in all future scenarios.

Marine Mammals

Northern Walrus

Northern walrus show small declines under the low hunting scenarios, but cannot withstand a doubling of harvest levels (figure 4.2). However, there is also a bottom up impact from climate change indicating walrus are sensitive to both top down and bottom up changes. Under the L1H1 scenario the biomass decreases by 11% with a small increase in mortality from $0.173y^{-1}$ to $0.186y^{-1}$. There are slight to moderate decreases in the biomass of prey groups ranging from 3% for echinoderms to 27% for other benthos (figure 4.6). Under the high climate scenario, H1H2, these declines increase to a minimum of 14% for bivalves to 42% for other benthos. When comparing all scenarios for northern walrus (figure 4.2), changes in climate do appear to be responsible for some of the declines along with harvesting. Biomass decreases by 51% for the H1H1 and H2H1 scenarios (high climate with low and high variance coupled with constant harvest rates), which is higher than the low climate scenarios with constant harvest rates of 11% indicating that there is still a substantial decline in this population due to bottom

up forces (roughly 40%). However under the high hunting scenario, H1H2 ending mortality increases to $3.170y^{-1}$, and with all high hunting scenarios the biomass is reduced by 99-100%. As killer whale biomass was forced to emulate increased sightings in both scenario (thereby having identical results for killer whales), the cause of the increased mortality is due to a doubling of harvest levels. Although population levels increased by 26% from 1970-2009 (chapter 2) this population is not able to withstand current harvest rates, and a doubling of harvest is detrimental to the population.

Ringed Seals

The ringed seal group is shown to benefit under all scenarios. When comparing the L1H1 and L1H2 scenarios the biomass increases from 29% to 64% with total mortality remaining relatively constant even under higher harvest (figure 4.7). The ringed seal's most significant predators are polar bears. However under all scenarios all polar bear groups decline nearly 100% removing this group as a source of mortality¹¹. Therefore removal of ringed seals through increased harvest was not enough to suppress populations at the same level caused by polar bears. Compensation for declines in sculpins/zoarcids and gadiformes in the diet was provided by increases in sandlance and capelin groups.

Narwhal

Recreation of the past HB ecosystem identified past slight declines in narwhal (14% decline from 1970-2009). However, current results for future simulations indicate narwhal cannot withstand increases in mortality from the starting value of $0.088y^{-1}$ to $0.185y^{-1}$ for the L1H1 scenario and $3.016y^{-1}$ for the H1H2 scenario. Similar to ringed seals, the largest contributors to the diet show changes with decreases in sculpins/zoarcids and gadiformes, with increases in capelin and sandlance. Yet, whereas ringed seal biomass increases, narwhal biomass declines by 59% for the L1H1 scenario and 97%

¹¹Foxe Basin polar bear catches were simulated as relative catches rather than forced due to only a small population being located within the area.

4.4. Results

for the H1H2 scenario due to the high mortality. It should be noted there appears to be a rebounding of the population under the H1H1 and H2H1 scenarios, due to increased predation of ringed seals by killer whales. As the ringed seal population increases, they make a larger contribution to the diets of killer whales, thus decreasing the predation on narwhal. The predation mortality remains at an increased level of 48% (figure 4.8) indicating that as the population decreases, predation mortality caused by killer whales does not increase further.



Figure 4.6: Changes in biomass for northern walrus with important contributors to diet and mortality. S (mortality at the start of the model 1970) is presented along with E (mortality at the end of the scenario simulation). Ending values for biomass, mortality, and catches are averaged over the last 10 years of the simulation. Open circles represent initial biomass for the Ecopath model (1970 value), while the shaded circles represent the ending biomass and are scaled to represent the percent change in biomass. *Indicates ending biomass is reduced by 100%

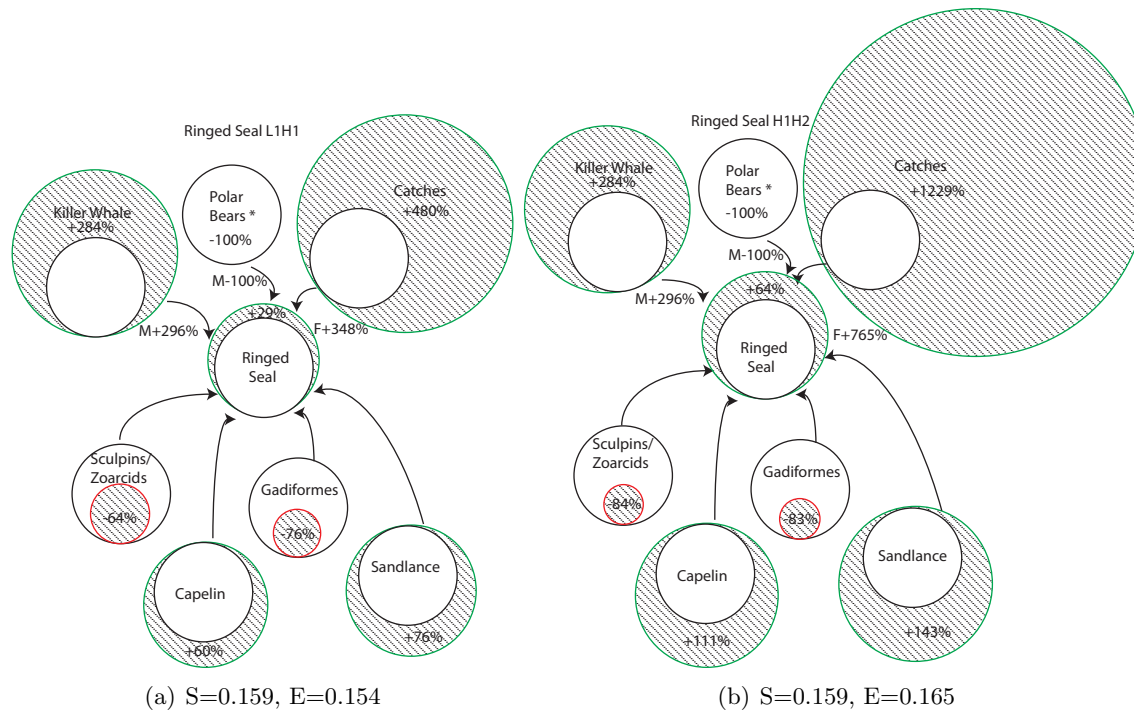


Figure 4.7: Changes in biomass for ringed seals with important contributors to diet and mortality. S (mortality at the start of the model 1970) is presented along with E (mortality at the end of the scenario simulation). Ending values for biomass, mortality, and catches are averaged over the last 10 years of the simulation. Open circles represent initial biomass for the Ecopath model (1970 value), while the shaded circles represent the ending biomass and are scaled to represent the percent change in biomass. *Indicates ending biomass is reduced by 100%

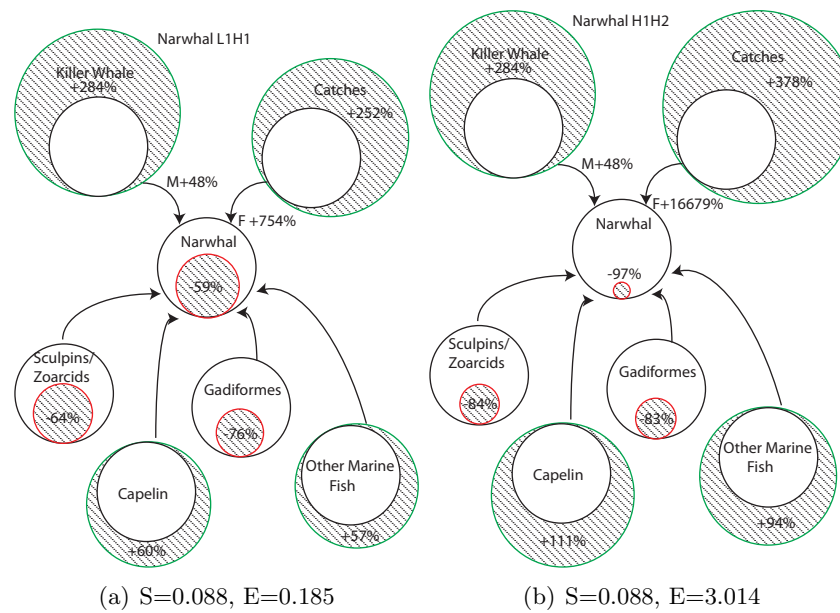


Figure 4.8: Changes in biomass for narwhals with important contributors to diet and mortality. S (mortality at the start of the model 1970) is presented along with E (mortality at the end of the scenario simulation). Ending values for biomass, mortality, and catches are averaged over the last 10 years of the simulation. Open circles represent initial biomass for the Ecopath model (1970 value), while the shaded circles represent the ending biomass and are scaled to represent the percent change in biomass.

Other Marine Mammals and Birds

Current harvest levels of some marine mammals cannot be sustained until the end of the model simulation causing the biomass of these groups to decline to or near a biomass of $0t \cdot km^{-2}$. Declines of all polar bear groups was due to high mortality rates caused by harvest (figure 4.11) as this is their only source of mortality within the model. Eastern Hudson Bay beluga also follow this pattern, where constant continued harvest at the current level cannot be sustained. Starting mortality for this group was $0.069y^{-1}$ and increases to roughly $3y^{-1}$ by the end of the high hunting scenarios. The southern walrus ending mortality is very high ($3-3.5y^{-1}$) compared to the 1970 value of $0.097y^{-1}$. Past simulations indicate a decline of 10%, but the level of harvest cannot be maintained until the end of the model simulation.

Harbour and harp seals follow trends similar to ringed seals. With an increase in prey, and declines in some predators (polar bear populations) the populations grow. While there is harvest of these groups, the mortality is not enough to suppress these populations. Bearded seals do not follow this pattern in the model as they are unable to withstand the increase in mortality. Diet of bearded seals includes a larger component of benthic prey items indicating there may be some bottom up driven changes to the population. Mortality increases from the 1970 value of $0.176y^{-1}$ to roughly $0.23y^{-1}$ and $0.43y^{-1}$ under the low and high harvest scenarios respectively (figure 4.9). Bearded seals already showed declines from 1970-2009, thus indicating previous hunting mortality was high. Killer whales were forced within in the model, as sightings have increased, but at a rate much higher than captured by the past model. Therefore the population was kept constant at the 2009 level (with large increases in the past, see appendix A) for future simulations.

While prey for the bowhead population increases (zooplankton), mortality rates remaining stable throughout all scenarios. As harvest for this group is low, there is potential for the stock to increase under all scenarios. Since the mortality rates are not significantly affected by increases in harvest, changes to bowheads are being caused by increases in prey avail-

ability. This is also the case for James Bay and western HB belugas. Both beluga groups increased during 1970-2009 with a continued trend into the future simulations. These groups differ from the eastern HB beluga in that the starting hunting mortality is much lower, and these two populations are large enough to withstand continued harvest rates within the model.

The seabird group increases range from 8% to 15% for the low climate scenarios and from 34% to 40% for the high climate scenario. Mortality increases slightly under all scenarios, but as this model group has a diverse diet, there is the ability to compensate for loss of benthic food sources to more pelagic based ones.

4.5 Discussion

Climate forcing in the model is taken from coupled models incorporating atmosphere, ocean, and sea ice models to make predictions based on climate change scenarios (GFDL, 2010). The "Low climate" scenario in this model should be considered conservative, as under this scenario greenhouse gas emissions are assumed to remain constant at 2000 emission levels, something which has already been surpassed by present day greenhouse gas levels. Even the high climate scenario depicted by the IPCC scenario A1B could be considered moderate, as ice still reaches a maximum ice cover albeit for much shorter time periods than other scenarios. For Hudson Bay it is believed that sea ice will disappear with a doubling of CO_2 (Gough and Wolfe, 2001), an occurrence for all future states predicted by the IPCC (IPCC, 2007), with the exception of the constant 2000 emission scenario. It should be noted that these models may underestimate the impacts of greenhouse gas loading, meaning that decreases to sea ice may occur faster than modeled (Stroeve et al., 2007). Some models predict the Arctic will undergo near ice-free summers by the year 2040 (Holland et al., 2006) or between 2050-2100 (Stroeve et al., 2007). Previous IPCC models failed to capture the extreme ice minimum of 2007, as unexpected and large scale fluctuations in climate are possible (ACIA, 2004). Preliminary evidence from the IPCC Fifth Assessment suggests predictions of temperature increases will be more

extreme than predicted by climate models used in this study (Glikson, 2011; Mah, 2011).

Although drivers (SST and sea ice cover) have been shown to cause expected changes to Hudson Bay for past simulations, their ability to represent all aspects of climate change is limited. Factors such as snow cover, solar radiation, freshwater inputs, stratification, and ocean circulation all play a role in determining types and amounts of production (Stewart and Barber, 2010; Taucher and Oschlies, 2010). However the linkages of these factors to species within the Hudson Bay ecosystem are limited. They have been excluded not as oversight, but rather due to lack of understanding to the large scale implications to the system. As more studies are completed in the future, additional information can be incorporated into the model to capture a wider array of environmental variable and their impacts on production.

Producers

Changes to the composition of producers occur under all scenarios with pelagic production increasing and ice algae decreasing. While changes to individual producers may appear extreme, total production increase is more modest ranging from 15% to 18% from the 1970 values accounting for both producer groups. Studies from 1998-2003 for Arctic primary production show increases of 30% attributed to a tripling of CO_2 (Pabi et al., 2008), while future projections indicate a further increase of 20 to 30% in high latitudes (Richardson, 2008), indicating model estimates may be low as they also include future changes. For the Atlantic Ocean future changes in CO_2 are predicted to increase production by 15 to 19%, although when accounting for other climate changes the overall increase is likely to be lower (Hein and Sand-Jensen, 1997). Hudson Bay is not as productive as high Arctic areas but the changes to primary producers suggested by the model appear to be on par with reported and predicted values for other high latitude areas.

Benthos

Declines in benthic biomass are attributed to the reduction in ice algae detritus within the model. This implies that benthos are reliant on detrital matter sinking during the spring melt of sea ice. Stable isotope studies in Norway identify ice algae as the main food item for benthos, and changes in climate reducing their preferred food source could alter distribution and abundance of benthos with far reaching ramifications to higher level predators (McMahon et al., 2006). In productive Arctic areas chlorophyll a (Chl a) is significantly correlated to benthic biomass (Chukchi Sea), with declines in carbon flux to benthos causing declines in standing stock biomass of 50% from 1998-2004 (Bering Sea) (Dunton et al., 2005; Grebmeier et al., 2006). However, in less productive marine regions, such as the Beaufort Sea, this relationship between Chl a and benthic biomass is not as strong as in high productive areas (Dunton et al., 2005). The link between ice algae and benthic biomass has not been identified for Hudson Bay as there are no comprehensive studies to show changes in ice algal biomass (or even standing stock of total production for the whole region). However, sea ice algae are a major component of biomass in first year Arctic sea ice (Riedel et al., 2006). Investigation of benthos in Arctic glacial bays reveals climate warming will lead to declines in biodiversity (Wlodarska-Kowalczyk and Weslawski, 2001). While the details within this model are not precise enough to model finer resolution changes, the fact that certain species groups fare better than others indicates there will be some changes to benthic composition and most likely diversity as well.

Zooplankton

Increases in zooplankton groups in the model were driven by increases in pelagic production which peaks between June and September depending on the model scenario (figure 4.1). In the northwest Atlantic, freshening of the ecosystem is believed to cause greater phytoplankton production and a reorganization of zooplankton favoring smaller shelf associated copepods (Pershing et al., 2005; Greene and Pershing, 2007). While different zoo-

plankton species are predicted to react differently, changes in climate are expected to cause general changes in distribution, assemblages, abundance, timing of life history events, and spatial match-mismatch with predators (Gremillet et al., 2008; Richardson, 2008).

Trophic mis-match between timing of zooplankton and phytoplankton blooms was not accounted for within the model, although timing of some zooplankton blooms are driven by temperature, whereas phytoplankton blooms are driven primarily by light (see Richardson, 2008, for a summary of zooplankton studies). Temporal scale of annual blooms for phytoplankton or zooplankton is not tuned to species specific information, and therefore does not account for the effects of changes in the spring bloom-zooplankton peaks and the consequences to zooplankton populations. As zooplankton groups are aggregated in the model, more information will be necessary to expand the model groups for a greater understanding of specific species. Inclusion of region specific information on zooplankton responses to climate change would likely suggest which species will succeed and which will decline. This might also entail a restructuring of the functional groups within the model to highlight key indicators to climate change. However, as only two zooplankton surveys have been completed to date within Hudson Bay (Harvey et al., 2001, 2006) information of this quality is not likely to be available in the near future.

Fish

Fishing mortality contributes a small percentage to total fish mortality (less than 1% contribution to total mortality in most cases) indicating bottom up changes in the food web (i.e., changes in benthos and zooplankton populations) have a greater effects over biomass than harvest rates. While initial fish catches were estimated based on per capita rates (Booth and Watts, 2007, and chapter 2), and increased with human population growth, it is possible they are underestimated due to under reporting or low initial per capita estimates. However when harvest rates were doubled in the model simulations some species were able to continue to increase. In general, Arc-

tic herring and cod fisheries are predicted become more productive under climate change, with declines to freshwater fisheries (ACIA, 2004). Past fisheries attempts have not shown to be profitable in Hudson Bay (Stewart and Lockhart, 2005) due to accessibility and costs associated with fishing in this region. If these hindrances decline in the future, model results identify fishing effort should be focused on species predicted to increase in the future such as capelin, sandlance, and to a lesser quantities, Arctic charr. These species all display low harvest mortality compared to total mortality indicating there is the potential to increase harvest beyond the High harvest scenario levels without compromising the future biomass levels.

Marine Mammals

Other studies have assessed the future impacts of climate change on marine mammals, sometimes with conflicting results (Burek et al., 2008; Ferguson et al., 2005; Laidre et al., 2008; Moore and Huntington, 2008; Huntington, 2009). Polar bears and narwhal appear to be the most sensitive of all Arctic marine mammals to climate change due to specialized feeding, dependence on sea ice, and small sub-populations, while ringed seals and bearded seals have large circumpolar populations making them considered less sensitive (Laidre et al., 2008). Ice breeding pinnipeds (harp, ringed, bearded seals and walrus) will likely experience declines due to ice melt and retreat of ice shelves, unless they adapt to breed on land (Moore and Huntington, 2008). Polar bears are the only group to include an ice-mediation function within the model (appendix A), specifying that prey becomes less vulnerable as sea ice declines. Although changes in polar bear foraging ability affecting fitness have been well documented (Stirling and Derocher, 1993; Lunn et al., 2002; Stirling, 2002; Stirling and Parkinson, 2006), the importance of hunting mortality in the model far surpasses mortality caused by changes in the food web. The model simulations highlight the high harvest rates of other marine mammal stocks as well (narwhal, eastern HB beluga, walrus). As future simulations cannot be verified, research into sustainable harvest levels for these species in particular would be useful in preventing over harvest.

It is anticipated that nutritional stress will become an issue as marine mammal and bird diets shift away from Arctic cod to less energetically rich species (Tynan and DeMaster, 1997; Gaston et al., 2005; Burek et al., 2008). However in the model, diets of many piscivorous predators shift from Arctic cod, polar cod, sculpins and zoarcids to capelin and sandlance. Energetic values of fish taken from Newfoundland and Labrador regions show a value of 4.4 kJg^{-1} for Arctic cod and sandlance, with a higher energetic value of 8.4 kJg^{-1} for capelin (Lawson et al., 1998). Although values are not available for all prey items, capelin energetic values are higher than Arctic cod and sandlance are of comparable nutritional value. Thus, shifts in predator diets including these species may not alter their overall nutritional levels. This does not account for spatial availability of prey, as in reality changes in distributions may make prey unavailable. Rather if prey are available nutritional values suggest capelin and sandlance are suitable energetic substitutes to Arctic cod.

Key Uncertainties

The model identifies that certain groups can increase based on increasing food supply and decreasing predation. Many other factors may affect survival and should be studied carefully. The model does not account for factors which may affect breeding or reproduction as they are not well understood, but they should be considered when assessing future threats to any species group in the region. The most prominent changes to zooplankton from climate change include shifts in distribution with the general movement towards poles and earlier peaks in abundance (Richardson, 2008). Endemic species will have to compete with northward moving migrant species in addition to new invaders such as gelatinous zooplankton which may become prominent (Gradinger, 1995; Brodeur et al., 1999). Fish and invertebrates are predicted to have moderate local extinctions, invasions, and species turnover (Cheung et al., 2008). While Hudson Strait contains colder deeper water compared to HB, it may be acting as a thermal barrier to prevent temperate species from entering the area. Reduction of sea ice over

time in Hudson Strait is believed to have allowed killer whales to access Hudson Bay (Higdon and Ferguson, 2009), thus potentially opening Hudson Bay and other high latitude regions to more temperate marine mammals shifting poleward (Kaschner et al., 2011). As Hudson Strait warms further, colder water currents may also be less effective at preventing invading zooplankton and fish species. For invasive species, thermal tolerances and quality of prey are important factors that should be incorporated into future models. Spatial components may alter results if prey are located only in specific areas within Hudson Bay. While the implications of climate change and removal of top predators are considerable (increased contaminants, invasive species, alterations to metabolic rates, changes in quality of prey items, etc.), we present the results of this model to be used as a tool to identify important stressors and their likely impacts to the Hudson Bay region.

General Conclusions

While there are multiple effects of climate change, some of which are accounted for within the model, the main results indicate the importance of harvest on marine mammal populations. Harvest rates must be decreased within the model in order to see environmental influences on higher trophic levels. As hunting has the greatest effect on marine mammal populations, efforts will need to focus on decreasing harvest limits, if managers want to maintain the structure of these marine mammal populations. Hunting pressure on vulnerable stocks (walrus, narwhal, eastern HB beluga, polar bears, and bearded seals) should be reduced in the immediate future to avoid extirpation. The socio-economic ramifications to Inuit in Hudson Bay should be considered in the context of reducing or ending the harvest of these species. Yet, alternative protein sources are generally poor in quality, expensive, and do not benefit the health of northerners as do traditional foods (Loring, 1996; Tait, 2001; Freeman, 2005).

Fishing may become more desirable since predator release by declining marine mammals may make fishing activities more lucrative than in the past. Model simulations highlight marine mammal and fish species (ringed

seals, western HB beluga, sandlance and capelin) able to increase under a doubling of present day harvest rates and changes to the food web. It is possible to consider that if harvest of vulnerable species is reduced, compensation could be allowed by increasing harvest on more stable species groups. Additional species specific modelling would be useful to assess the potential for changes in harvest levels at a finer scale. Furthermore, it may be a controversial option as the diet of Inuit in the region has been centered on marine mammals for thousands of years (Stewart and Lockhart, 2005). Community willingness to adhere to policy options and enforcement may be difficult. However, these issues need to be weighed heavily against the desire to prevent the extirpated of marine mammal populations.

4.6 Hudson Bay Biomass and Morality Figures

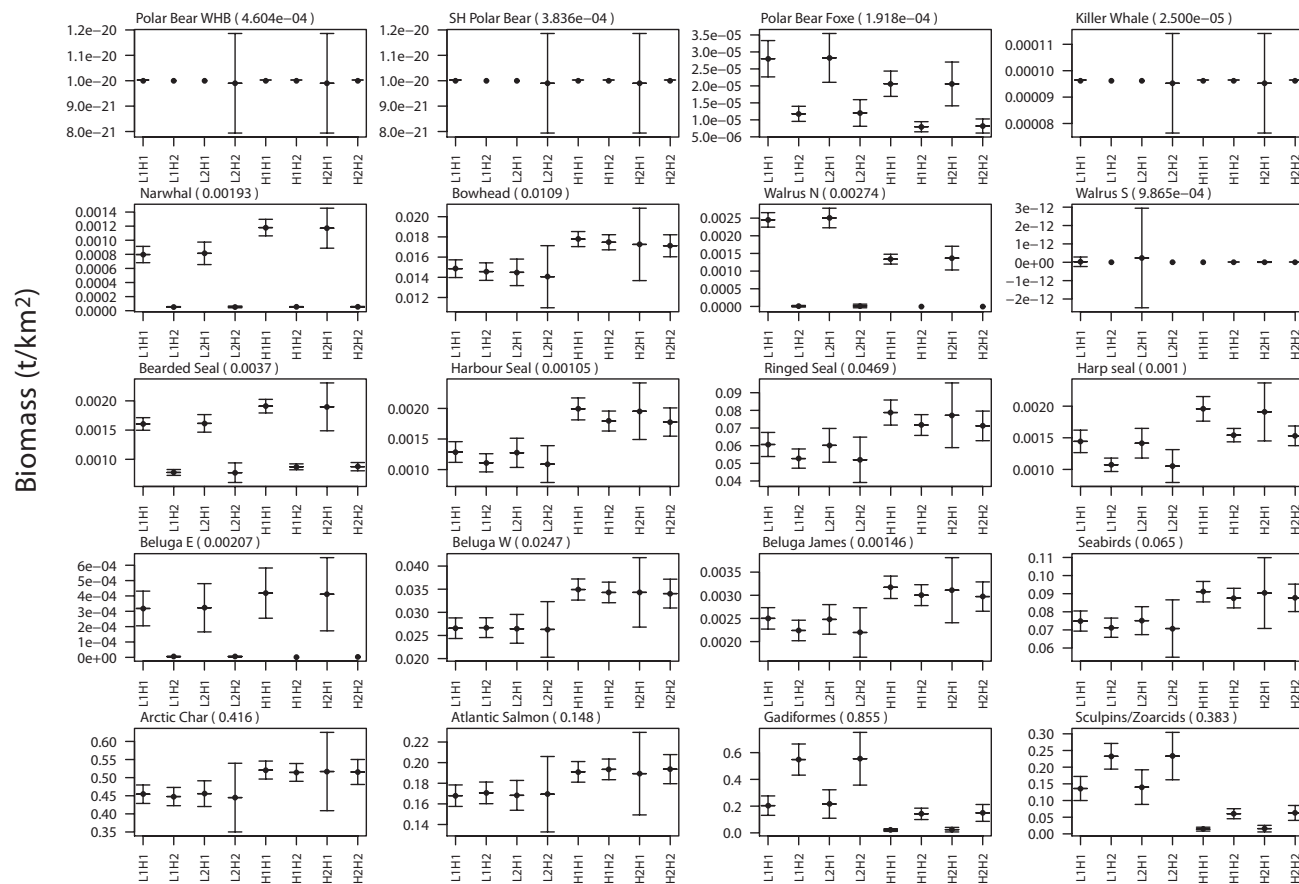


Figure 4.9: Ending biomass by species group for each simulation scenario. Values represent the mean and 95% CI for the last 10 years of each simulation. Biomass for the first year of simulation is presented above the graph in parentheses for comparison.

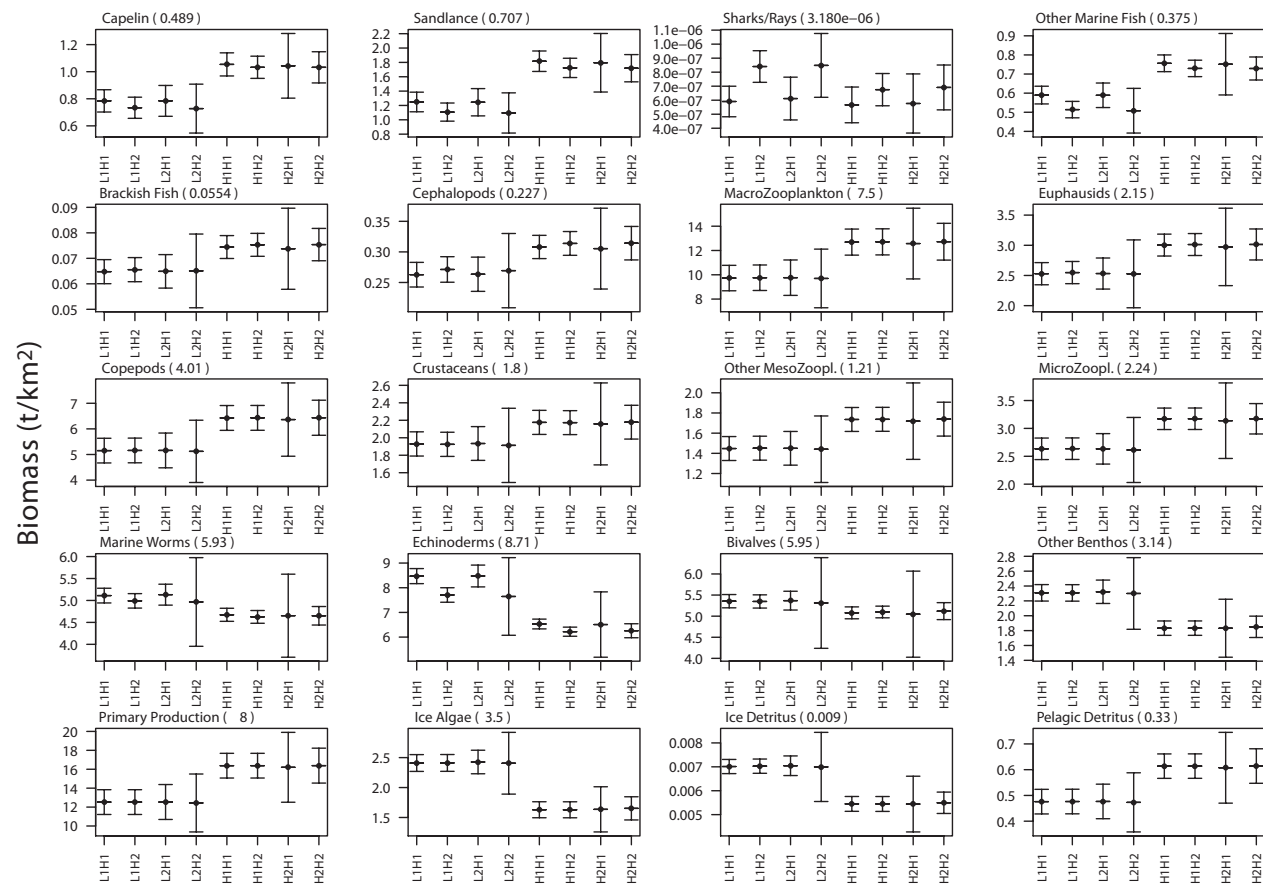


Figure 4.10: Ending biomass by species group for each simulation scenario. Values represent the mean and 95% CI for the last 10 years of each simulation. Biomass for the first year of simulation is presented above the graph in parentheses for comparison.

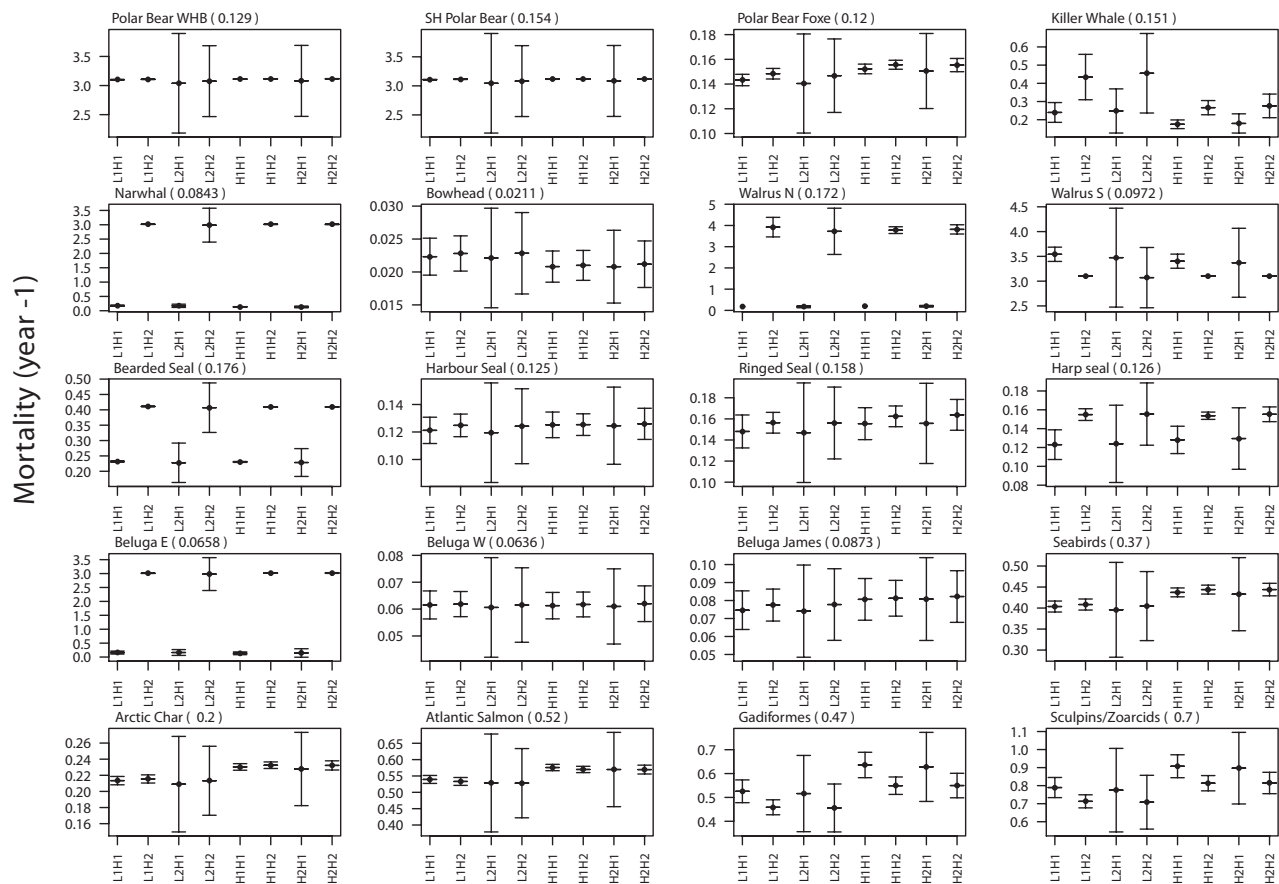


Figure 4.11: Ending mortality by species group for each simulation scenario. Values represent the mean and 95% CI for the last 10 years of each simulation. Mortality for the first year of simulation is presented above the graph in parentheses for comparison.

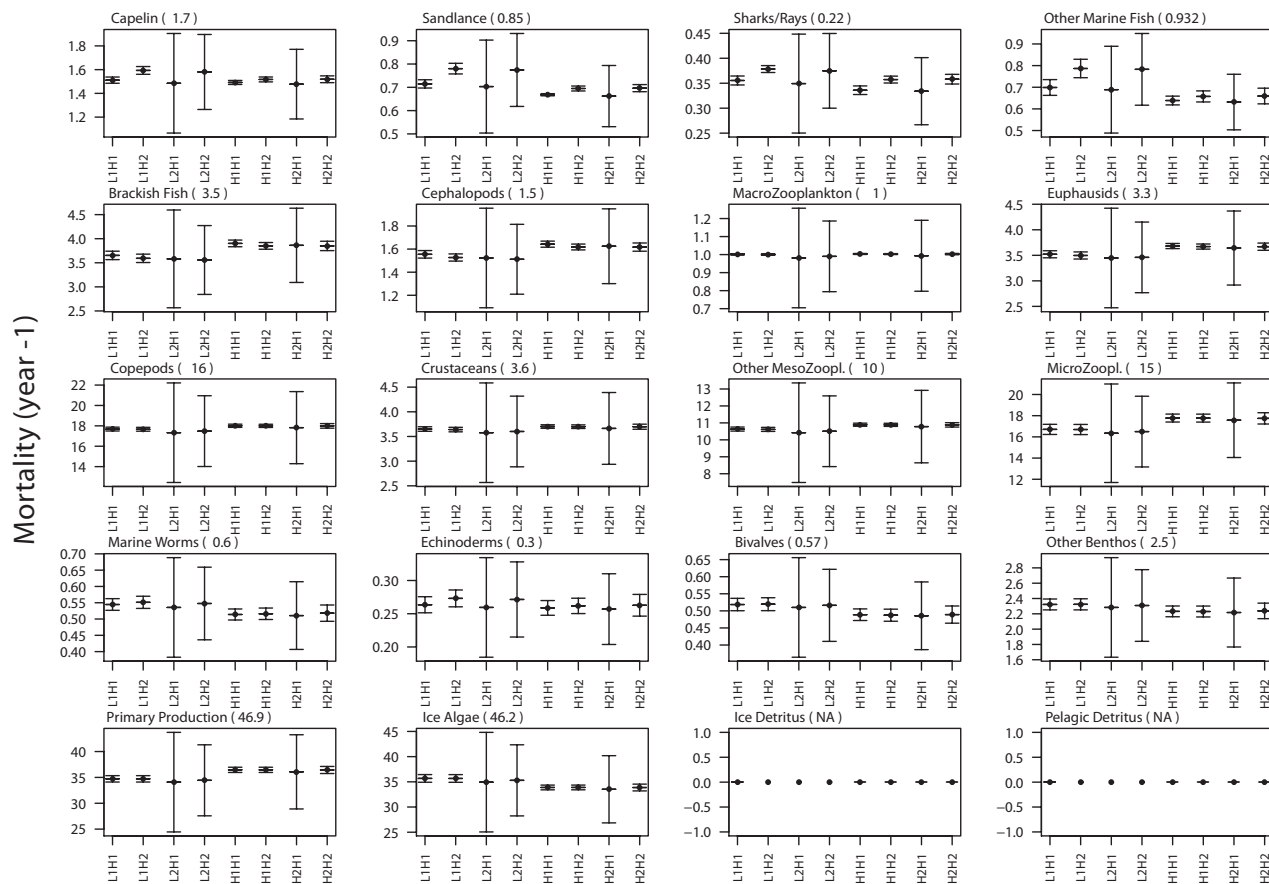


Figure 4.12: Ending mortality by species group for each simulation scenario. Values represent the mean and 95% CI for the last 10 years of each simulation. Mortality for the first year of simulation is presented above the graph in parentheses for comparison.

Chapter 5

Future Impacts of Fishing and Climate Change on the Antarctic Peninsula Marine Ecosystem

5.1 Synopsis

This chapter focuses on future simulations of the Antarctic Peninsula ecosystem, utilizing the past model simulations in chapter 3 to continue harvest and climate trends into the future. In keeping with chapter 4, data from global climate models representing future IPCC climate scenarios were used to continue model drivers into the future. These were combined with harvest scenarios representing 2007 levels (the last year of the past model simulation), and continued harvest at the quota level. Further development of harvest scenarios explores the effect of harvesting sexually immature krill on the structure of the ecosystem. Declines in sea ice, detritus, ice algae, and krill caused by warmer climates are responsible for most of the changes to the food web. Future scenarios identify copepods as the potential dominant zooplankton, filling the ecological role of krill within the model. More extreme climate and harvest scenarios result in an overall increase in trophic level for the ecosystem, attributed to diets shifting away from the less available ice algae and detritus, and re-focusing on more available zooplankton species. Krill is a main component to many predator diets, and continuing the harvest of krill may directly cause large declines in predators, but

it will contribute to decreasing a continually strained resource in the future.

5.2 Introduction

At the present time, rapid changes in climate are occurring in a short geological time frame, as indicated by unprecedented levels of methane and CO_2 in ice cores when compared to the last 420,000 years (Petit et al., 1999). Increased greenhouse gases are contributing to the overall warming of earth, with larger than average temperature increases observed at the Antarctic peninsula (Anisimov et al., 2001; Hansen et al., 2006a). Global, large scale changes will occur with continued warming of the Antarctic and the rest of the planet. Increased Antarctic temperatures have been linked to global sea level on geological time scales, through ice volume changes (Rohling et al., 2009). The West Antarctic Ice Sheet (WAIS), covering the western portion of the continent, would cause global increases in sea level 4-6m if it collapsed (Oppenheimer, 1998). While there is some thickening of the WAIS in the west, it is likely as a whole the ice sheet is thinning (Rignot and Thomas, 2002). Changes to the WAIS are thought to be larger than for the East Antarctic Ice Sheet (Bindshadler, 1998), which is said to be stable (Sugden et al., 1993). Increases in greenhouse gases and temperatures globally, and at the Antarctic peninsula, have resulted in the recent loss of major ice sheets, many at rates much faster than predicted. For example, the Wordie, Wilkens and Larsen ice shelves at the Antarctic peninsula have all shown major reductions and collapses starting in the 1960s (Doake and Vaughan, 1991; Rott et al., 2002; Rignot et al., 2005).

The loss of sea ice at the Antarctic Peninsula has been shown to alter the flow of nutrients to top predators. Years with high sea ice (high-salinity water) favor diatom blooms where energy is then transferred to krill *Euphausia superba* and then further up the food chain (Marschall, 1988; Loeb et al., 1997; Moline et al., 2000; Atkinson et al., 2004). Low ice years (low salinity and increased glacial meltwater) favor smaller cryptophytes, which are then efficiently grazed by salps *Salpa thompsoni* (Moline et al., 2000, 2004). Declines in krill have been linked to poor reproductive success for

Adelie penguins and Antarctic fur seals Hofmann et al. (1998); Brierley and Reid (1999), however declines likely occur in other undocumented species as well.

In addition to the stress of a changing environment, krill (*Euphausia superba*) is harvested primarily for aquaculture feed, although products for human consumption and pharmaceuticals do exist (Nicol and Endo, 1999; Kawaguchi and Nicol, 2007). The quota for krill has increased from 1.5 to 4 million tonnes between 1991 and 2000, although CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) applies a precautionary approach to the management of Antarctic krill such that only roughly 9.1% of the total biomass may be harvested (Hewitt et al., 2002; Nicol and Foster, 2003). This value is intentionally set low to ensure that predator demands are met, and krill biomass does not drop below 20% of the unexploited biomass (Hewitt et al., 2002). However, issues of spatial overlap indicate that krill predators and fisheries may be in competition regarding the timing and location of acquiring krill (Reid and Croxall, 2001; Hewitt et al., 2004). The subdivision of catches into smaller areas or "Small Scale Management Units" has been proposed decrease fishery pressure in concentrated areas (Hewitt et al., 2004). There is a discrepancy between the actual harvest levels of roughly 100,000t compared to the potential quota levels of 4.89 million tonnes (Nicol and Foster, 2003). A "trigger level" of 620,000t exists for the Atlantic sector, meaning if this level is reached within any fishing area (such as all sub-areas within area 48), catches within the area should be further subdivided (Antarctic and Southern Ocean Coalition, 2010). Krill catches in 2010 increased to 210,000t, roughly double the 1994-2009 catches (Nicol et al., 2012). Recent CCAMLR documents indicate the trigger level needs re-assessment as it was established in 1991 because krill fishing effort is excessively concentrated in coastal areas (Antarctic and Southern Ocean Coalition, 2010).

Recent expansions in krill based products for pharmaceuticals, health food products and aquaculture feed are likely to increase pressure on the fishery (Nicol et al., 2012). Krill in the aquaculture market is expected to continuing growing with increased demand for krill in aquaculture feeds

(Gascon and Werner, 2006). Because catches are lower than quota levels the aquaculture industry views krill as having an unexploited biomass (Olsen et al., 2006). It has been demonstrated it is a suitable substitute for traditional fish meal for farmed Atlantic salmon (Olsen et al., 2006), and contains the desirable long-chain omega-3 polyunsaturated fatty acids that consumers favor in fish products (Naylor et al., 2009). The number of krill-related patents has increased every year from 1976-2008, with most patents related to krill products for human consumption, and Japan as the country having lodged the most patents (Nicol and Foster, 2003).

Recreation of the past Antarctic peninsula ecosystem through the use of an ecosystem model suggests that environmental factors have been more significant than harvest in determining krill and krill-predator biomass (Chapter 3). The model shows that increasing the harvest of krill from past levels of roughly 100,000 tonnes for area 48.1 to the quota of 625,000 tonnes (Hewitt et al., 2002) does not bring about significant changes to the trophic structure of the ecosystem. It should be noted, however, that harvest rates are only assessed on a temporal scale in this model and trophic structure will likely show higher sensitivity to harvest on a spatial scale. Since increasing harvest levels in combination with changes in climate will potentially alter the ecosystem, scenario simulations using this ecosystem model have been employed to assess potential future states of the ecosystem. As some life stages of krill are linked to sea ice for food and protection (Marschall, 1988; Daly, 1990), and krill are directly harvested, this central link in the ecosystem will face multiple stressors. This modeling exercise aims to identify vulnerable linkages in the ecosystem in addition to identifying the strongest factors for change.

5.3 Methods

Model Structure

Using the previously constructed EwE model for the Antarctic Peninsula (chapter 3), various scenarios of climate change and harvest levels were

simulated to assess the impacts on the ecosystem. Continuing from the past model, where known trends were recreated, this chapter focuses on increasing stressors and the trophic implications.

Some minor adjustments to the model (chapter 3) were made in light of more recent literature. Immigration rates for chinstrap and gentoo penguins were removed based on longer timescale data indicating that their populations are not increasing at the Antarctic Peninsula (Trivelpiece et al., 2010), contrary to the previous belief that they were increasing partly due to immigration from other regions (Fraser et al., 1992).

The past model was forced with environmental drivers and harvest. Harvest rates were taken from recorded CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) catches in the past (CCAMLR, 2008b). Environmental drivers were selected as forcing functions for primary producer groups in addition to mediation functions¹².

Ecosim simulations used the Ecopath with Ecosim software (Christensen et al., 2005; Buszowski et al., 2009), where temporal changes in biomass are calculated using equations 2.3 in chapter 2 at each time step in the model. Once simulations were completed the trophic level of the ecosystem (TL_E) and the trophic level of catches (TL_C) were calculated using equations 2.6 and 2.7 from chapter 2.

Ice cover is included in the model as a driver of the ice algae and diatom functional groups. Ice algae refers to the algal cells frozen within the sea ice that remain overwinter as a potential food source for some stages of krill (Marschall, 1988; Arrigo et al., 1997). Diatoms can also survive within the sea ice, but were given their own functional group due to their importance to zooplankton species. They are also favored in cooler years, contributing to pelagic blooms during spring melts (Legendre et al., 1992; Varela et al., 2002; Garibotti et al., 2003; Moline et al., 2004). SST (sea surface temperature) was chosen as a driver for cryptophytes and other phytoplankton functional

¹²Forcing functions act as a multiplier to trends over time for the producer groups, while mediation functions act as an indirect link between species groups. For example in the past model, the presence of ice reduces the vulnerability of some krill stages to predators, as they have been observed to hide in ice crevasses (Marschall, 1988).

groups, primarily to fit the salp functional group better, whose abundance patterns are linked to warmer waters (Atkinson et al., 2004; Pakhomov and Froneman, 2004). Increased biomass of cryptophytes has been linked to warmer years and lower salinity water (Moline et al., 2000, 2004).

For the past model, SST (sea surface temperature) and ice cover (% of model area covered) were used to force different primary producer groups and mediation functions for krill and salps. Continuing the model into the future was accomplished through extending environmental time series. Data was extracted from future climate models and combined with past model data for SST and ice cover to provide an extended dataset covering 100 years. Combining past simulations with different levels of future model forcing, allowed simulations previously ranging from 1978-2007 to extend to 2077.

Environmental drivers

To assess future ecosystem state two climate scenarios were combined with three harvest scenarios. The climate scenarios are based on low and high climate projections for the Antarctic Peninsula using the global GFDL CM2.1 coupled model (GFDL, 2010). For the 'Low' climate scenario the IPCC Constant 2000 emissions scenario was used, where greenhouse gas emissions are set to the year 2000 emission levels with global changes to environmental parameters considered conservative. While this target has already been surpassed in reality, it serves as a conservative estimate to system dynamics. The 'High' climate scenario for the model employed the A1B IPCC scenario, whereby future emissions are a result of a balanced energy future (IPCC, 2000). As with chapter 4 the A1F1, B2 and A1 scenarios were considered before selecting the A1B as the 'High' climate change scenario. However, due to challenges in accessing data and reliability of climate model outputs, the A1B scenario gave more extreme ice loss in future simulations, so it was selected. Ice and SST trends for past and future states are presented in figure 5.1. The past ice and SST data extracted from the global HadISST (Hadley Centre Sea Ice and Sea Surface Temperature model) at the British

Atmospheric Data Centre (BADC, 2010), and combined with the future data to allow the model to run from the past through present day and into the future.

In order to assess the potential for increased variance in future environmental factors, two levels of variances were applied to each climate scenario (Low and High). A constant variance scenario (Low) used variance based on past data to assume variance in future data is not any higher or lower than past changes. Using a normally distributed multivariate covariance matrix generated from past data, variance was applied to the future time series of SST and ice cover. 100 draws of variance created 100 scenarios with the same mean values to allow the model to be run for 100 simulations for each scenario. Next, for the variance was doubled (High variance), while mean trends remained the same to account for the possibility of increased variance in the future. Labels for the variance in the model are referred to numerically as 1 or 2, so a Low climate scenario with variance based on past values would be referred to as the L1 climate scenario while doubling the variance would be referred to as the L2 scenario.

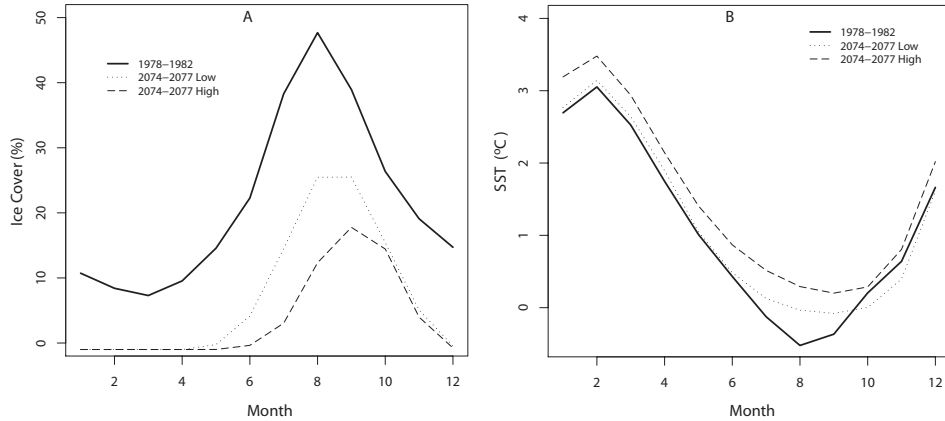


Figure 5.1: Sea ice and SST data used for model simulations. Past values were extracted from the HadISST global model (BADC, 2010). Future ice and temp data was extracted from the GFDL CM2.1 coupled model (GFDL, 2010).

Harvest Levels

Each of the climate scenarios was combined with krill and fish harvest at varying levels. The first scenario, the 'Low Harvest' (H1) scenario combines past harvest trends with future catches constant at 2007 harvest levels for all species harvested (table 5.1). The catch from 2007 is kept constant from 2008-2077 to identify the long term effects of current harvest levels. In some cases, where fish species were not harvested every year, the highest value identified from a five year time span (2003-2007) (CCAMLR, 2008b) was continued into the future. In addition, harvest for some fish species no longer occurs. In these cases, no catches were used in future scenarios. Krill are harvested every year, therefore the 2007 value remained constant for the 'Low Harvest' scenario. The second harvest scenario considers the effects of higher landings for both fish and krill. Under this scenario, krill catches are increased to operate at the current quota level, while fish catches are doubled from their 2007 values (or values used in the "Low Harvest" scenario). This "High Harvest" (H2) scenario, is then further broken down into two subroutines. The first (H2a) assumes all krill catches are taken from the adult krill stage and the second (H2b) splits the krill catches into the adult and juvenile stages. In reality both juvenile and adult krill are harvested with larger krill being more valuable. Quality of harvested krill is graded by length, with krill $>45\text{mm}$ earning the highest value and krill $<35\text{mm}$ earning the lowest (Ichii, 2000). Length of krill in Polish catches in southwest Atlantic sector of the Antarctic ranged from 25-60mm in the late 1990s, with a majority of the catches $>35\text{mm}$ (Jackowski, 2002). For the H2b scenario, 75% of catches were assumed to be from the adult krill group, while 25% were from the juvenile krill group, to explore the effects of harvest at different life stages. Catches and harvest mortalities for each scenario are presented in table 5.1.

Table 5.1: Summary of harvest values and hunting/fishing mortalities used for the initial Ecopath model (1978), and future hunting scenarios: H1 where catch and effort are constant to 2007 values, and H2 where catches and effort are doubled from the 2009 values. Fishing mortality for future scenarios is calculated using the 2007 biomass for each species group.

Species Group	Catch $t \cdot km^{-2}$				Fishing Mortality (y^{-1})			
	1978	H1	H2a	H2b	1978	H1	H2a	H2b
krill adult	0.055	0.100	0.923	0.692	0.006	0.016	0.146	0.110
krill juvenile	0.018	0.033	-	0.231	0.001	0.002	-	0.013
<i>C. gunnari</i>	1.00E-05	2.53E-05	5.06E-05	5.06E-05	3.45E-05	1.64E-04	3.28E-04	3.28E-04
<i>N. gibberifrons</i>	1.00E-05	2.98E-06	5.96E-06	5.96E-06	1.23E-05	4.48E-06	8.97E-06	8.97E-06
<i>P. antarticum</i>	1.00E-05	2.08E-05	4.16E-05	4.16E-05	8.00E-06	2.16E-05	4.32E-05	4.32E-05
Other Icefish	1.00E-05	4.46E-06	8.92E-06	8.92E-06	2.97E-05	1.70E-05	3.40E-05	3.40E-05
lg noto	1.00E-05	1.49E-05	2.98E-05	2.98E-05	1.69E-05	3.06E-05	6.13E-05	6.13E-05
sm noto	1.00E-05	1.19E-05	2.38E-05	2.38E-05	2.93E-05	4.06E-05	8.12E-05	8.12E-05
myctophids	1.00E-05	-	-	-	5.41E-05	-	-	-
other pelagics	1.00E-05	1.49E-06	2.98E-06	2.98E-06	2.04E-05	3.76E-06	7.52E-06	7.52E-06
toothfish	1.00E-05	-	-	-	2.16E-04	-	-	-

5.4. Results

Table 5.2: Simulations of varying levels of climate and hunting. Scenario names indicate levels of hunting and climate. First letter indicates either a Low (L) or High (H) climate scenario followed by the variance applied to the climate data (either past variance (1) or double the past variance (2)). The second letter indicates the level of hunting applied to the simulation; H1 for constant hunting at the 2007 levels, or H2 for harvest at quota levels.

Climate Scenario	Variance	Hunting Scenario	Scenario Abbreviation
Low	Normal	Constant 2007	L1H1
Low	Normal	Double adult	L1H2a
Low	Normal	Double adult/juvenile	L1H2b
Low	Doubled	Constant 2007	L2H1
Low	Doubled	Double adult	L2H2a
Low	Doubled	Double adult/juvenile	L2H2b
High	Normal	Constant 2007	H1H1
High	Normal	Double adult	H1H2a
High	Normal	Double adult/juvenile	H1H2b
High	Doubled	Constant 2007	H2H1
High	Doubled	Double adult	H2H2a
High	Doubled	Double adult/juvenile	H2H2b

5.4 Results

General Results

All future scenarios reveal declines for ice-associated producers ice algae and diatoms. The other phytoplankton group increases in all future scenarios with cryptophytes showing mixed results. Declines in the biomass of cryptophytes under future scenarios is attributed to increased predation mortality rates, caused primarily by salps. Detritus shows moderate declines ranging from 58% to 70% for the L1H1 and H2H2a scenarios. Decline in detritus is caused by declining primary production, and overall lower biomass of the ecosystem, both of which feed into the detritus pool. Total primary production declines 63% for the L1H1 scenario and 68% for the H2H2a scenarios, with all scenarios falling in the range of 54% to 75% declines. Figure 5.2 identifies all changes to functional groups by scenario in reference to the original 1978 starting biomass.

Increasing the effects of climate change does show some alterations to the ecosystem. The H2b harvest scenario (75% harvest of adult krill and 25% harvest juvenile krill) has the largest confidence intervals under each climate scenario for both biomass and mortality. Most species across all trophic levels show largest CI for H2b harvest scenarios, especially when combined with High variance in climate models (L2 and H2 scenarios). High variance climate scenarios coupled with harvest of juvenile krill cause large ranges of future ecosystem states, as CI for some groups are larger than the mean biomass for some groups (diatoms, cryptophytes, copepods, microzooplankton, and krill groups) (see figure 5.15 for all scenario results). It is important to note the harvest of adult krill is higher for the H2a harvest scenario, therefore removal of adult krill is not the cause of the large variance.

The highest biomass of krill (adult and juvenile groups combined) in future scenarios is under the L1H1 and L2H1 scenarios, in which harvests are the most conservative of any future scenarios combined with less variance in environmental drivers. However, under these scenarios declines of combined adult and juvenile groups are roughly 75% from their starting biomass, indicating while the scenario structure may be conservative, the results and impacts to the ecosystem are not.

Results are presented by trophic groupings with key species highlighted. For these selected species scenarios L1H1, H2H2a and H2H2b are represented graphically to highlight changes to the most important contributors to diet and mortality.

Changes in Ecosystem Biomass and Trophic Levels

Overall there are large declines in the total biomass of the ecosystem compared to the starting values (table 5.3). The Low climate scenarios show higher ending biomass than the High climate scenarios with the exception of the H1H2b and H2H2b scenarios. This is due to further declines of species caused by increased climate scenarios. The higher biomass in the H1H2b and H2H2b scenarios is an artefact of the large variation in biomass the lower trophic levels. Trophic Level (TL) of the ecosystem shows slight increases

in most future scenarios when compared to past and present values. This is due to the fact that the TL of most functional groups increases at varying degrees in the future simulations. The loss of producers may alter diets to shift to higher trophic levels when primary production is not available, thus increasing the TL of organisms.

The TL of catches decreases from the starting value of 3.39 to a value of 2.34 for 2007 (the ending year of the past model), before continuing to increase under all future scenarios. The high starting value is a reflection on the fish contribution to catches in the past model. A combination of krill and fish were harvested, with fish groups having higher trophic levels than krill (adult krill TL=2.53, juvenile krill TL=2.25 for 1978). At the end of the past simulation, TL of catches is at the lowest value, as krill contributed largely to the total of all species harvested thus reducing the overall TL of catches. In future scenarios, krill continue to be a major contributor to the total catch, however TL of catches is increasing. This is due to the overall TL of krill increasing. Mean TL of adult krill as averaged over the last 10 years for each scenario ranged from 2.71-2.95, while juvenile krill ranged from 2.40-2.75 indicating krill are feeding at a higher trophic level. This is most likely explained by a reduction of primary production (primarily ice algae and diatoms) in the diets of krill at various stages, being replaced by higher TL zooplankton species, such as copepods or micro-zooplankton.

Table 5.3: Trophic level of ecosystem (TL_E) and catches(TL_C) for the Eco-path model (1978) and each simulation. Results presented are averages values for the last 10 years of each simulation. Total biomass and total catch are presented in $t \cdot km^{-2}$ for all species within the ecosystem.

	TL_E	TL_C	Biomass
1978	1.91	3.39	209.73
2007	1.98	2.34	134.97
L1H1	2.02	2.68	119.56
L1H2a	2.05	2.78	130.06
L1H2b	2.01	2.74	113.76
L2H1	2.02	2.64	117.50
L2H2a	1.98	2.79	107.90
L2H2b	2.05	2.80	161.02
H1H1	2.10	2.74	99.25
H1H2a	2.07	2.88	102.21
H1H2b	2.15	2.89	144.23
H2H1	2.08	2.74	98.82
H2H2a	2.05	2.87	105.33
H2H2b	2.12	2.86	154.31

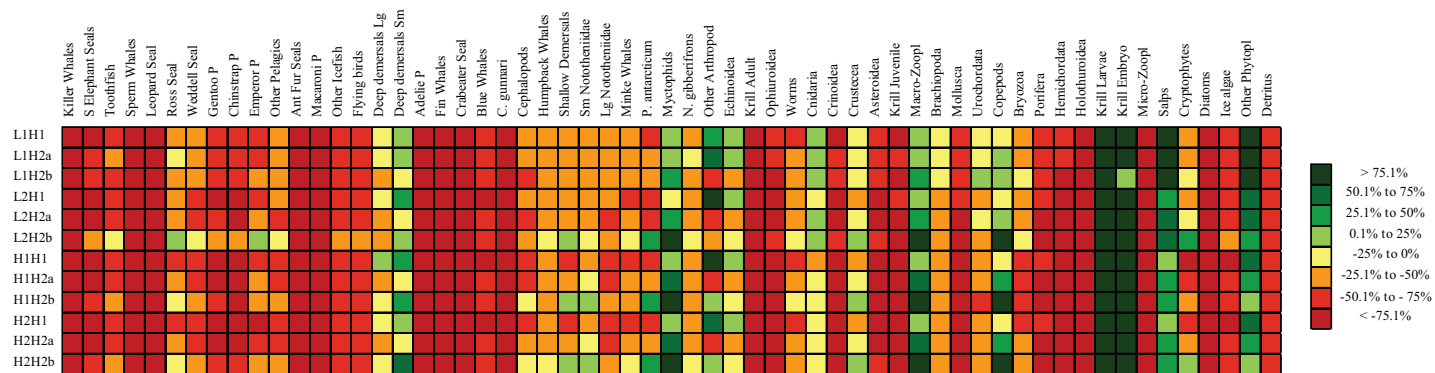


Figure 5.2: Changes in biomass by species group for each future scenario. Represented values are presented as the mean biomass of the ending values for each scenario as averaged over the last 10 years of the simulation.

Producers and Detritus

Total primary production declines in all future model scenarios. Although there are increases in the 'other phytoplankton' group, all other producers decrease. This is expected for ice algae and diatoms as they are driven with a sea ice forcing function. However, as cryptophytes and other phytoplankton groups are driven with SST, we would expect the cryptophytes to increase. Cryptophytes had the smallest starting biomass of all producers (in 1978). Increases in salps, who feed efficiently on these smaller producers contribute to large increases in total mortality for cryptophytes. Even though the drivers forcing this group are increasing in magnitude, effects of predation mortality are greater, causing overall declines (figure 5.18). Detrital groups also show declines, with the general trend of biomass decreasing further from the Low to High climate scenarios. This is caused by less contributions to detritus from producers and other organisms as their biomasses have declined.

Zooplankton

Copepods

For copepods, the biomass decreases slightly (13%) for the L1H1 scenario, although it increases by 45% and 193% for the H2H2a and H2H2b scenarios. For reference the ending biomass for the H2H2b scenario averaged $57\text{t}\cdot\text{km}^{-2}$ compared to the starting biomass of $19\text{t}\cdot\text{km}^{-2}$. Mortality decreases under all scenarios from the starting values due to decreases in predation, as copepods are not harvested (figure 5.3). Declines in the L1H1 scenario are caused by the declines in ice algae, diatoms, and micro-zooplankton prey items. While micro-zooplankton and diatoms remain near absent in the H2H2a scenario, copepods increase. This is a result of further declines in predation from krill groups, and a slight increase in ice algae contribution to the diet. Under the L1H1 scenario, there are higher biomasses of other functional groups, thus higher predation levels from these groups, in conjunction with less ice algae available to copepods. Under the H2H2a scenario the contribution

of ice algae increases when compared to the L1H1 scenario. This increase continues with the H2H2b along with further declines in krill and other predators resulting in a tripling of biomass. Under the H2H2b scenario predation mortality caused by both adult and juvenile krill is greatly reduced (100% declines for both groups). This is especially important for the juvenile krill as they have the highest predation mortality on copepods at the start of the model. For copepods the L2H2b and H2H2b scenarios have high variance in the biomass results (figure 5.15), which is an important reason for the variation in higher level species such as some fish and marine mammals.

Krill

Future impacts to krill populations come from two sources in the model. First, there are changes caused by food web interactions (declines in major contributors to the diet; ice algae and diatoms). Second, an ice-mediating function increases the vulnerability of larval and juvenile krill to predators as sea ice decreases (see appendix J for full details). As the krill embryo group represents a non-feeding stage before krill rise to the surface to feed, the diet of this group was considered as imported to the model. This allows for large increases in biomass of this group, based on the adult (sexually mature) population. A similar, but lower increase holds for the larval krill group. While there are almost certainly additional environmental factors contributing to the biomass of these groups, the increase in biomass under model scenarios should be considered optimistic. However, even as these groups increase, older stages of krill are not as successful in the simulated future.

Changes in juvenile krill for the L1H1 scenario are caused by bottom-up changes in the ecosystem. A decline in biomass by 77% occurs in this scenario, while total mortality declines slightly (figure 5.4). Declines in ice algae, diatoms and copepods as prey items are important. Ice algae is also included as a mediation function whereby its presence reduces juvenile krill's vulnerability to predators. However, as total mortality has not increased under this scenario, this is likely not an important contributor to

the decline. Under the H2H2a scenario juvenile krill biomass declines by 90% of the starting value (a further 13% from L1H1). There are no catches of juveniles in this scenario, but further reduction of adults is the reason for further declines. Total mortality is lower in this scenario, however adult krill biomass is further reduced. In the H2H2b scenario, juvenile krill continue to decline further to a 94% reduction from the starting biomass, even though copepods are increasing and ice algae declines are less than in previous scenarios. The further reduction is a result of direct harvest of this group with a larger fishing mortality ($0.54y^{-1}$ compared to starting value $0.01y^{-1}$) and an increased total mortality.

Total mortality for juvenile krill and adult krill are highest in harvest scenarios H2b (with the exception of L1H2b). In the Low climate scenario juvenile krill are able to withstand an increase in harvest. However the increased variability of the Low climate scenario and the high reduction of ice in the High climate scenario coupled with the direct harvest of juveniles increases mortality on juvenile krill more than double compared to the starting value. This is also reflected in the adult group, whereby the mortality is higher in these scenarios, even when less adult krill is harvested. There is less recruitment into the adult phase, as more juveniles are being harvested increases the mortality on the adult krill stage in these scenarios.

Adult Krill

For adult krill declines in biomass of 75% caused from the L1H1 scenario are a result of bottom up changes in the ecosystem. While the increase in fishing mortality appears to be large at 298% (increase from $0.01y^{-1}$ to $0.04y^{-1}$), total mortality in this scenario decreases from the starting value of $1.54y^{-1}$ to $1.32y^{-1}$ indicating changes are a result of bottom-up changes in the food web (figure 5.5). This is also in part by declines in lower stages of krill, which are impacted by sea ice through mediation functions. Under the H2H2a scenario adult krill biomass is further reduced as total mortality increases due to catches operating at current harvest quotas (with all catches from the adult krill groups). An important predator group, macro-zooplankton,

also increases. However predation mortality from this group is 10% lower at the end of the scenario than the 1978 starting value. The biomass of adult krill declines 92% under this scenario. However total mortality continues to increase under the H2H2b scenario, where 25% of the catches at quota level are taken from the juvenile krill group. Biomass of adult krill declines by 98%, even though there are increases in copepods and other phytoplankton, and a slight rebounding of ice algae under this scenario, and less adult krill are being harvested. Yet, the impact of harvesting juveniles increases the total mortality, causing the further decline of the adult biomass.

Salps

Salps show increasing biomass at varying levels in all future scenarios (figure 5.6). Prey items for salps are favored through the use of forcing functions; SST was used to force the cryptophytes and other phytoplankton groups, and a mediating function allowing greater foraging area for salps as sea ice declines. These groups are favored by increases in SST and contributed 65% of the total diet to salps at the start of the model. For the L1H1 scenario salps increase in biomass 75%. Although there is an overall slight increase in predation mortality, biomass is able to remain high. While salps generally contribute very little to the diets of other functional groups, their increasing biomass allows for increased predation, as other food items of predators are decreasing. Biomass patterns by scenario show increasing biomass as krill harvests increase from H1 to H2a to H2b (see figures 5.14 and 5.15).

In the H2H2a scenario, biomass of salps is lower (although still increasing). Total mortality is relatively constant, but changes to the diets include; slightly more cryptophytes available, more copepods available, and less other phytoplankton. The 'other phytoplankton' group contributes 35% of the total diet in the Ecopath model, but for future simulations the contribution can easily reach over 85% of the total diet. The lower salp biomass in the H2H2a and H2H2b scenarios is heavily reliant on the other phytoplankton biomass.

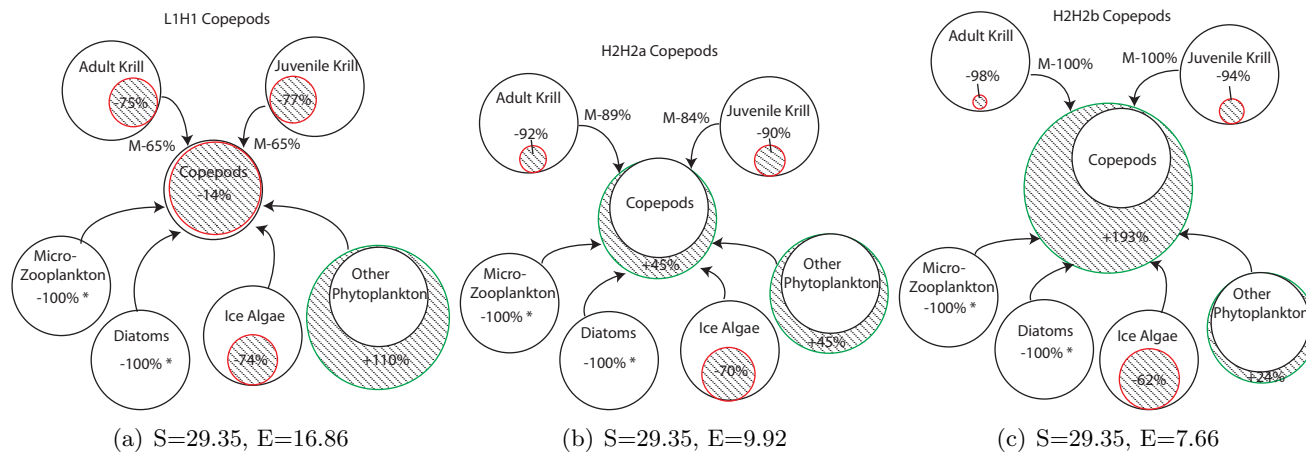


Figure 5.3: Changes in biomass for copepods with important contributors to diet and mortality. S (mortality at the start of the model 1978) is presented along with E (mortality at the end of the scenario simulation). Ending values for biomass and mortality are averaged over the last 10 years of the simulation. Open circles represent initial biomass for the Ecopath model (1978 value), while the shaded circles represent the ending biomass and are scaled to represent the percent change in biomass from the starting biomass of 100%. *Indicates ending biomass is reduced by 100%.

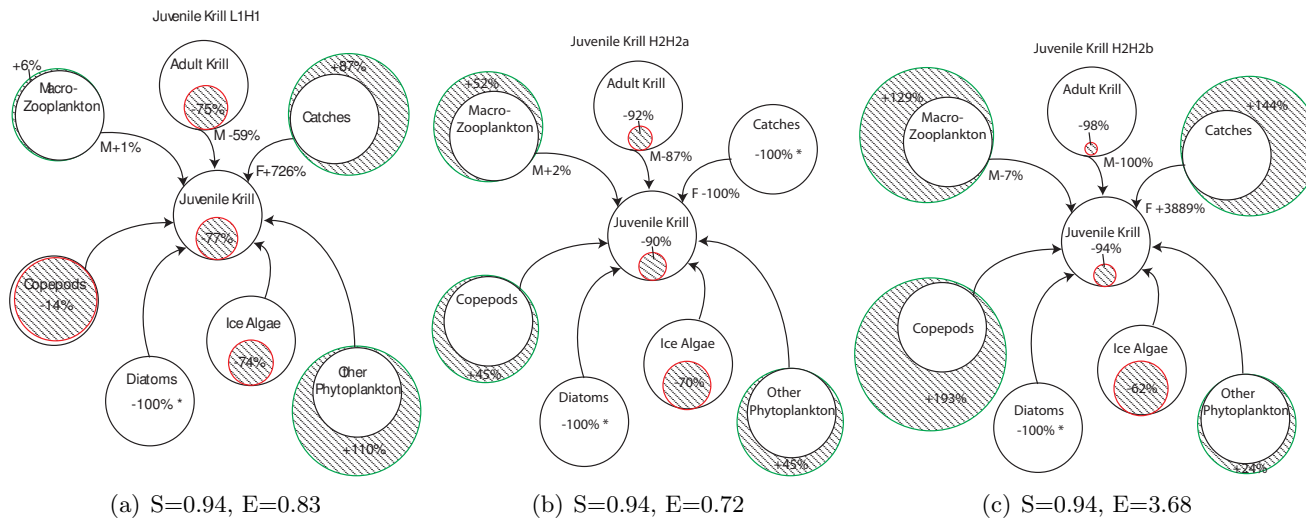


Figure 5.4: Changes in biomass for juvenile krill with important contributors to diet and mortality. S (mortality at the start of the model 1978) is presented along with E (mortality at the end of the scenario simulation). Ending values for biomass, mortality and catches are averaged over the last 10 years of the simulation. Open circles represent initial biomass for the Ecopath model (1978 value), while the shaded circles represent the ending biomass and are scaled to represent the percent change in biomass from the starting biomass of 100%.

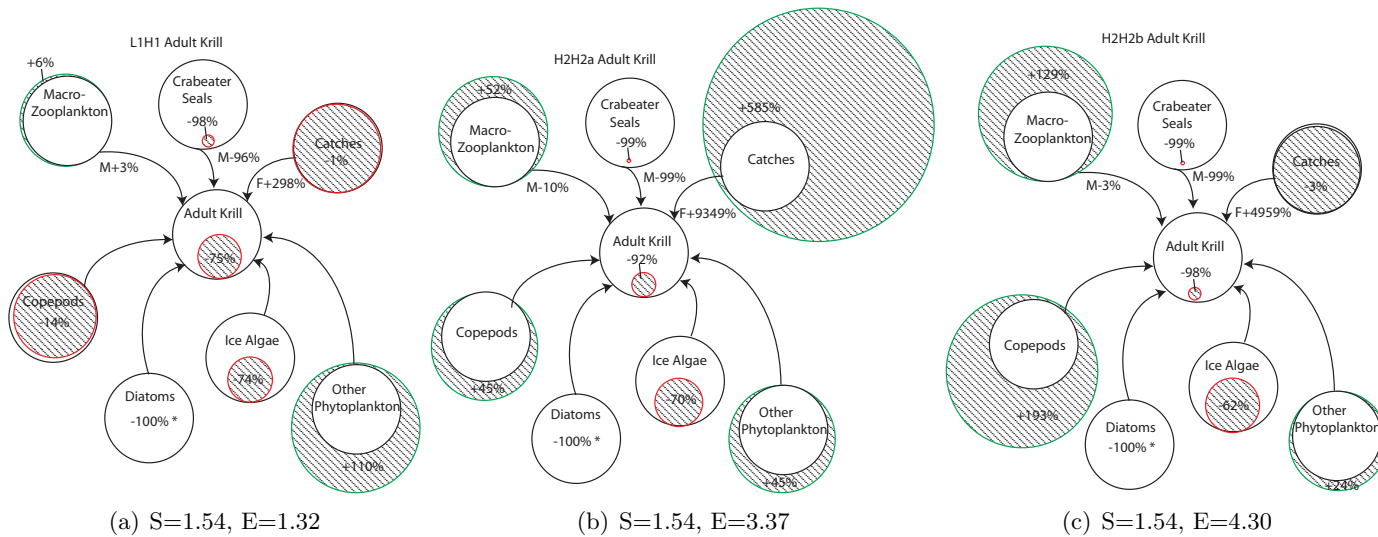


Figure 5.5: Changes in biomass for adult krill with important contributors to diet and mortality. S (mortality at the start of the model 1978) is presented along with E (mortality at the end of the scenario simulation). Ending values for biomass, mortality and catch are averaged over the last 10 years of the simulation. Open circles represent initial biomass for the Ecopath model (1978 value), while the shaded circles represent the ending biomass and are scaled to represent the percent change in biomass from the starting biomass of 100%. *Indicates ending biomass is reduced by 100%.

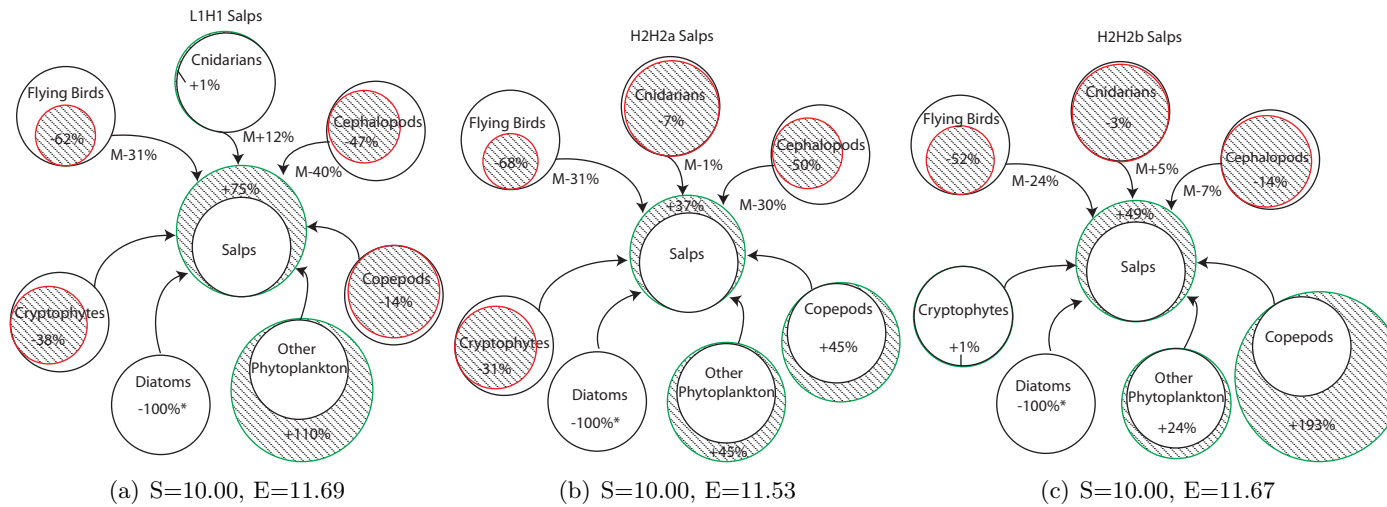


Figure 5.6: Changes in biomass for salps with important contributors to diet and mortality. S (mortality at the start of the model 1978) is presented along with E (mortality at the end of the scenario simulation). Ending values for biomass and mortality are averaged over the last 10 years of the simulation. Open circles represent initial biomass for the Ecopath model (1978 value), while the shaded circles represent the ending biomass and are scaled to represent the percent change in biomass from the starting biomass of 100%. *Indicates ending biomass is reduced by 100%.

Other Zooplankton

For the micro-zooplankton group biomass decreases due to increased predation mortality for all future scenarios. There is High variation in the L2 (Low climate double variance) scenarios, although mean biomasses remain quite low. Macro-zooplankton biomass increases in future scenarios while total mortality declines. The increase in biomass is possible as the contribution of other phytoplankton in the diet increases. The cephalopod group also shows declines in biomass and mortality indicating declines are driven by a lack of prey.

Benthos

All benthic groups show lower mortalities in all future model scenarios, due to declines in higher trophic levels. While most species decline in biomass due to reductions in detritus and ice algae, there are a few species that show increases in some scenarios (mostly the H2b scenarios). Cnidarians, crustaceans, other arthropods and echinoderms all have high contributions of other phytoplankton and macro-zooplankton to their diets at the end of future scenarios which allows for increases in biomass, as these groups are increasing. The remaining benthic groups have diets weighted more heavily on detritus, and thus are impacted through bottom up changes such as declines in detritus. Even though predation mortality is lower for these groups, prey items are reduced enough in the model to cause decreases in future biomass.

Fish

Myctophids

Myctophids are one of few groups to increase in biomass under future scenarios. Under all future scenarios total mortality decreases indicating a predator release may be causing the biomass to increase. However, under the L1H1 scenarios prey items are all declining as well, while biomass increases by 3% (figure 5.7). Less important prey items at the start of the model such

as macro-zooplankton increase in contribution to the diet of myctophids by more than double in future scenarios. In addition, myctophids are predated upon by many higher organisms, most of which decline substantially in the future. The relief in predation coupled with increases in copepods allows this group to increase. For the H2H2a scenario, a further decline in total mortality is observed in the model, with biomass increasing 70%. While adult krill and molluscs continue to decline, there is a slight rebounding of crustaceans, and an increase in copepods in conjunction with an increase in copepod contribution to the total diet. For the H2H2b scenario biomass of myctophids increases 176% from the starting value. This is caused by the large increase in copepods, which contributes 61% of the diet at the end of the scenario compared to 25% at the start (this is also the highest contribution of copepod to the diet compared to other scenarios). Crustaceans also show an increase in biomass as their diet in the future is heavily weighted on other phytoplankton and macro-zooplankton in this scenario in addition to the increase in the contribution to the diet. Crustaceans and copepods make up more than 86% of the ending diet. While total mortality is slightly higher than other scenarios (0.96 compared to 0.91 for L1H1, and 0.83 for H2H2a), it is still lower than the starting mortality of 1.35. In the model myctophids are able to increase through a combination of decreased predation, and increasing the contributions of available prey to the diet.

Deep Demersals Large

The large deep demersal group shows declines, although not as much as other fish groups. This is primarily due to a diet based more heavily on benthic species which do not decrease as much as pelagic species. A 9% decrease of large deep demersals for the L1H1 scenario further declines to 42% for the H2H2a scenario before increasing slightly to a total decline of 18% for the H2H2b scenario. Under the L1H1 scenario, major prey items decrease in biomass ranging from 27% for crustaceans to 77% for juvenile krill. Total mortality also decreases in this scenario as main predators are declining as well. The H2H2a scenario identifies further decline of predators and total

mortality in conjunction with larger declines in prey items with the exceptions of crustaceans. Crustaceans do increase in this scenario as previously mentioned due to the high percentage of other phytoplankton and copepods in their diets. For the H2H2b scenario the decline in large deep demersals is only 18% from the starting biomass, despite a slightly higher mortality than the other scenarios discussed. An increase in macro-zooplankton contribution to the diet occurs in the H2H2a and H2H2b scenarios. The rebounding in biomass for the H2H2b scenario is due to higher biomasses of important contributors to the diets (deep demersals small, macro-zooplankton and *P. antarcticum*) although they were not large contributors to the diet at the start of the simulation. The shift in the diets combined with higher biomasses of copepods and crustaceans in the H2H2b scenario prevent the larger declines as shown in scenario H2H2a.

Toothfish

Toothfish show large declines across all scenarios ranging from 37% for the H2H2b scenario to 55% for the L1H1 scenario (figure 5.9). Mortalities for all future scenarios are lower than the starting value indicating changes to toothfish are caused by bottom-up rather than top-down interactions. Catches for toothfish were set to 0 for the future simulations as they had only been harvested sporadically in the past (CCAMLR, 2008b). The H2H2b scenario has the highest biomass of toothfish when comparing the three scenarios, due to increases in small nototheniidae biomass (10%), and less severe declines of other important prey items. These four prey items remain the highest contributors to the diet for future scenarios with crustaceans as fifth, whose biomass also increases in the H2H2b scenario.

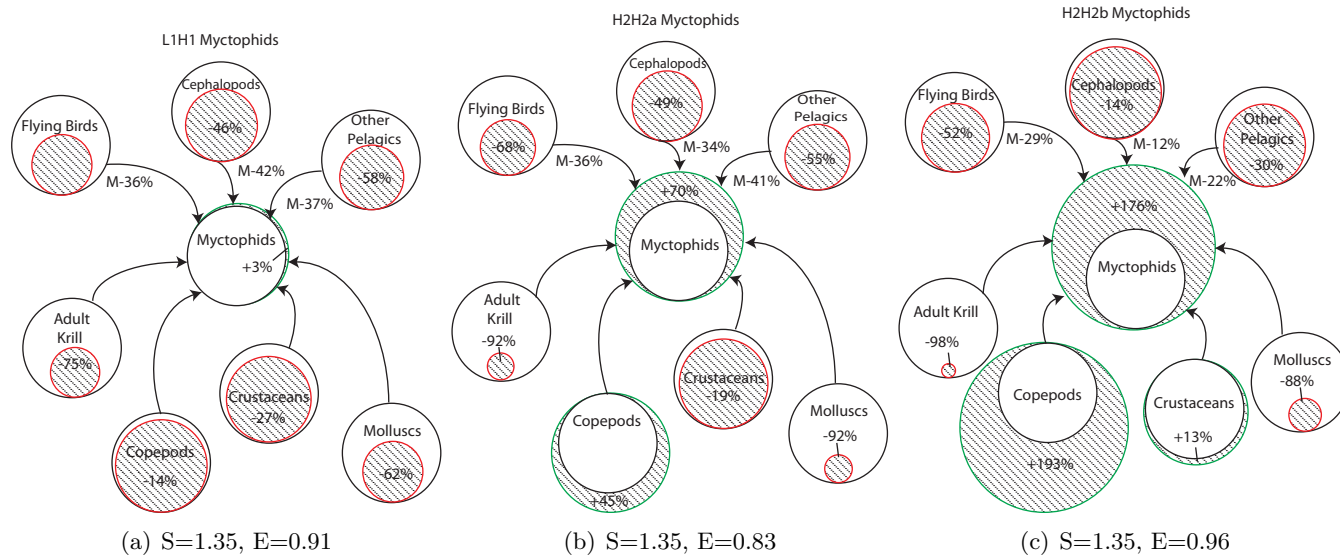


Figure 5.7: Changes in biomass for myctophids with important contributors to diet and mortality. S (mortality at the start of the model 1978) is presented along with E (mortality at the end of the scenario simulation). Ending values for biomass and mortality are averaged over the last 10 years of the simulation. Open circles represent initial biomass for the Ecopath model (1978 value), while the shaded circles represent the ending biomass and are scaled to represent the percent change in biomass from the starting biomass of 100%

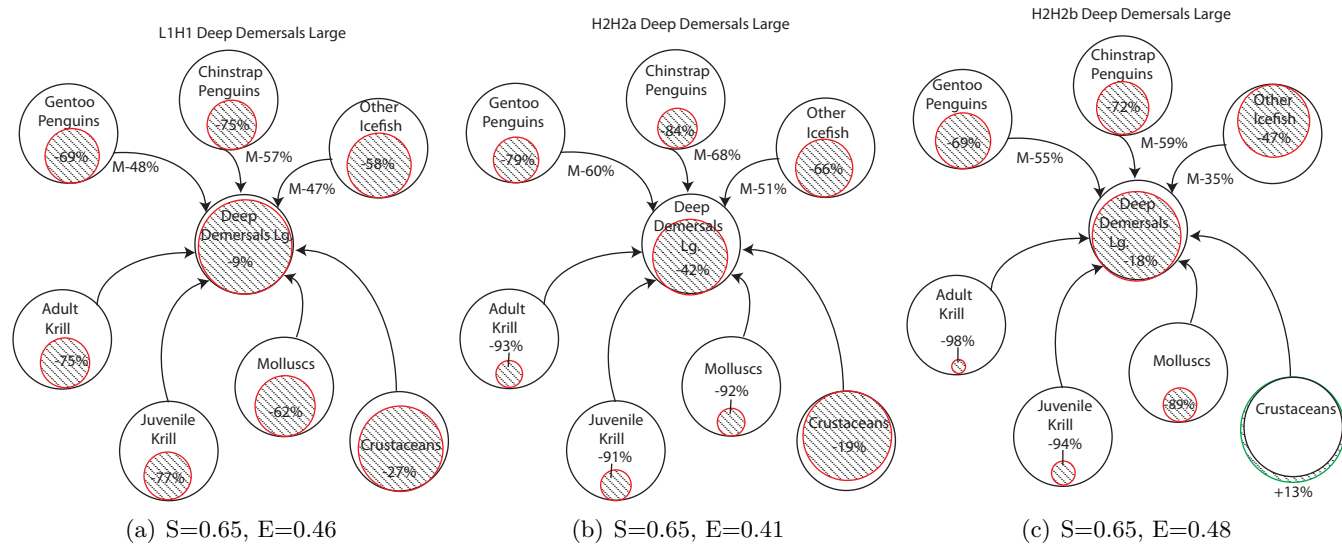


Figure 5.8: Changes in biomass for large deep demersals with important contributors to diet and mortality. S (mortality at the start of the model 1978) is presented along with E (mortality at the end of the scenario simulation). Ending values for biomass and mortality are averaged over the last 10 years of the simulation. Open circles represent initial biomass for the Ecopath model (1978 value), while the shaded circles represent the ending biomass and are scaled to represent the percent change in biomass from the starting biomass of 100%

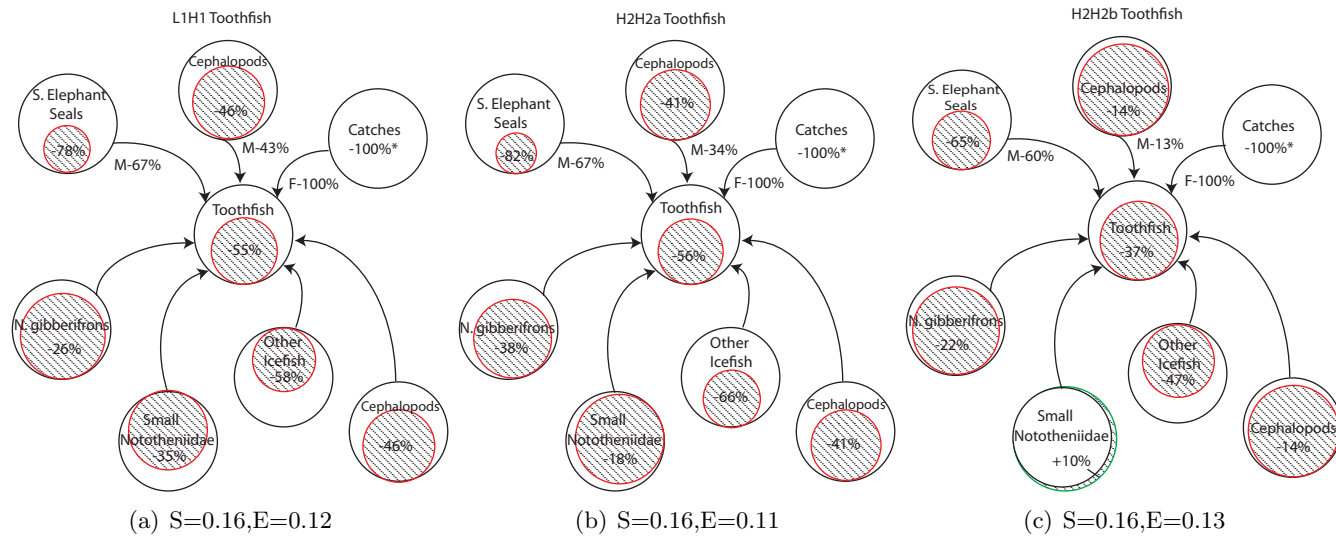


Figure 5.9: Changes in biomass for toothfish with important contributors to diet and mortality. S (mortality at the start of the model 1978) is presented along with E (mortality at the end of the scenario simulation). Ending values for biomass, mortality, and catches are averaged over the last 10 years of the simulation. Open circles represent initial biomass for the Ecopath model (1978 value), while the shaded circles represent the ending biomass and are scaled to represent the percent change in biomass from the starting biomass of 100%. *Indicates ending biomass is reduced by 100%.

Other Fish

The 'other pelagic' group, which is ecologically similar to the myctophid group, shows declines in biomass for future scenarios. Compared to the myctophid group, both groups have lower mortalities in the future due to declines in predators. However, diets of myctophids show a greater contribution to prey items favored under future scenarios; other phytoplankton, copepods and macro-zooplankton, while the other pelagic group has a higher contribution in the diets of declining species such as krill and cephalopods.

The small deep demersal group follows similar biomass patterns as the large deep demersal group, although increases are more extreme. Future mortality for this group is also reduced, but increases are driven by larger contributions to the diet for macro-zooplankton and crustaceans groups, both of which are increasing.

The large nototheniidae, small nototheniidae, *N. gibberifrons*, shallow demersals, and other icefish groups all show declines in biomass and mortality. Increased contributions of other phytoplankton, crustaceans and macro-zooplankton in these diets are identified for these groups, however initial diets in the Ecopath model contained moderate contributions from krill and crustacean groups. *C. gunnari* biomass declines while mortality increases in future scenarios. The starting diet of this group is also heavily weighted on krill and benthic invertebrates, most of which decline in the future. However, there is some top-down pressure from increased mortality from penguins, seals and other fish groups. *P. atarcticum* biomass and mortality both decline in future scenarios with the exception of the H2b harvest scenarios. As there are increases in contributions to copepods and crustaceans in the diet of *P. atarcticum*, biomass increases as these prey items also increase in these scenarios.

Birds

Adelie Penguins

Adelie penguins decrease due to bottom up changes in the food web. For the L1H1 scenario biomass is the highest of any other future states at a decrease of 75%, while the greatest decrease in biomass is observed for the H2H2b scenario at a 98% decrease (figure 5.10). Total mortality increases under this scenario, as the contribution of Adelie penguins to the diets of leopard seals increases. This is likely a result of other, smaller populations of penguins being less available to leopard seals, as they are declining due to diminishing food resources as well. Even under the L1H1 scenario, predation mortality of leopard seals increases by 123%, however total mortality only increases roughly 10% (from 0.29 to 0.31). It is likely that if enough resources were available, the Adelie penguin population could withstand a 10% increase in predation.

Other birds

Macaroni penguin biomass declines in future scenarios coupled with increased mortality, similar to the Adelie penguins. Predators of macaroni penguins also include killer whales and leopard seals, meaning increased mortality is caused by these groups. Flying birds along with emperor, gentoo and chinstrap penguins have quite large variances in biomass for the L2H2b scenario. While results for fish groups with similar patterns were attributed to large variations in copepods and macro-zooplankton, diets of penguins are more heavily weighted on cephalopods which also show this trend. However, macro-zooplankton are a key prey item for cephalopods, so the increased variation is in part due to the macro-zooplankton group. Biomasses for all of these groups decline in conjunction with lower mortalities in the future. Also worth noting is the increase in salp contribution to the diets of flying birds, chinstrap and gentoo penguins. Although the contribution to the diet was low in the Ecopath model (2% for chinstrap and gentoo groups and 5% for flying birds), it becomes the predominant

5.4. *Results*

contributor to diets in the future due to increased biomass in the model.

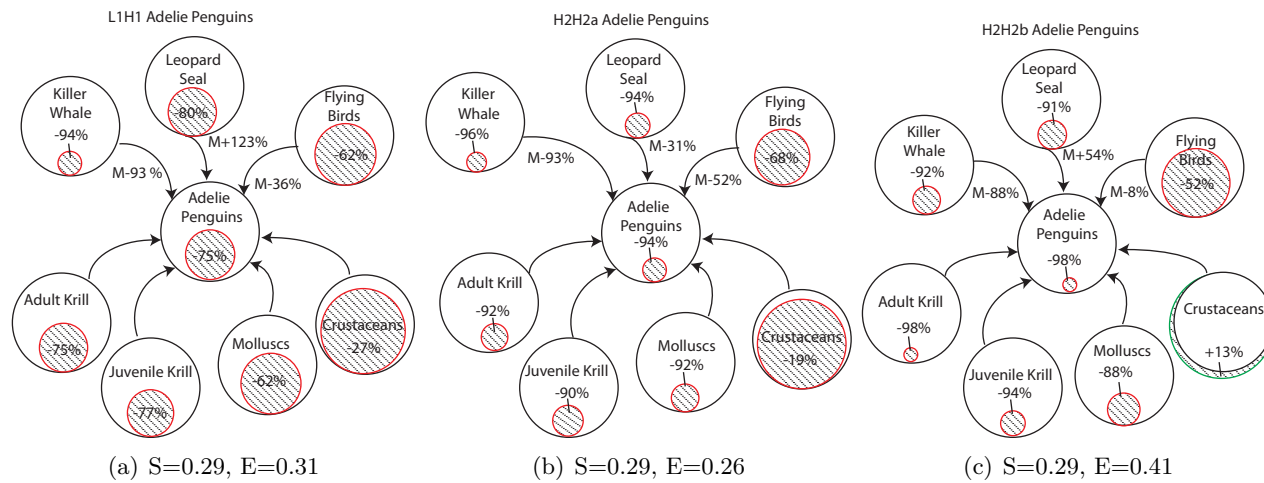


Figure 5.10: Changes in biomass for Adelie penguins with important contributors to diet and mortality. S (mortality at the start of the model 1978) is presented along with E (mortality at the end of the scenario simulation). Ending values for biomass and mortality are averaged over the last 10 years of the simulation. Open circles represent initial biomass for the Ecopath model (1978 value), while the shaded circles represent the ending biomass and are scaled to represent the percent change in biomass from the starting biomass of 100%

Marine Mammals

Minke Whales

Changes to minke whale biomass are driven from bottom-up changes in the ecosystem. Killer whales are the only predator, and biomass of this group declines over 90% from the starting biomass for all scenarios with predation mortality decreasing 90%, 87% and 88% for the L1H1, H2H2a and H2H2b scenarios respectively. If food resources were sufficient, release from predation mortality should cause an increase in whale abundance. However, there are large declines in the main prey species of minke whales. Of the four main prey items; adult krill, juvenile krill, copepods and micro-zooplankton, copepods are the only group to increase and only in select scenarios. For the L1H1 scenario, minke whale declines are caused by bottom-up factors (prey), as all main prey items are decreasing. In the H2H2a scenario minke whales decline slightly less (1%), even though copepod biomass shows an overall increase. This is not enough to compensate for the further reduction of krill. In the H2H2b scenario minke whale biomass is highest at a decline of only 23% from the starting value. Macro-zooplankton, a smaller contributor to the diet shows increases in biomass for the High climate scenarios, specifically the H2H2b scenario. Shifts from declining krill to increasing copepods and macro-zooplankton in the diet result in a less severe decline in this scenario.

Antarctic Fur Seals

Antarctic fur seals show large declines across all scenarios (figure 5.2). For the L1H1 scenario, declines are caused by declines in prey (figure 5.12). The two predators of fur seals; killer whales and leopard seals both decline themselves, as does the predation mortality caused by these groups. Even in scenarios where killer whale biomass is highest, but still lower than starting values, this is in combination with lower biomass values of leopard seals in these scenarios (figure 5.13). The largest contributors to the diet of fur seals; adult krill, juvenile krill, cephalopods and *N. gibberifrons* all decrease in all

5.4. *Results*

three scenario compared. While there are some differences in the degree of prey item declines, it appears as though reductions of prey items in the model are severe enough to cause declines of fur seals $>90\%$ for each of the scenarios presented.

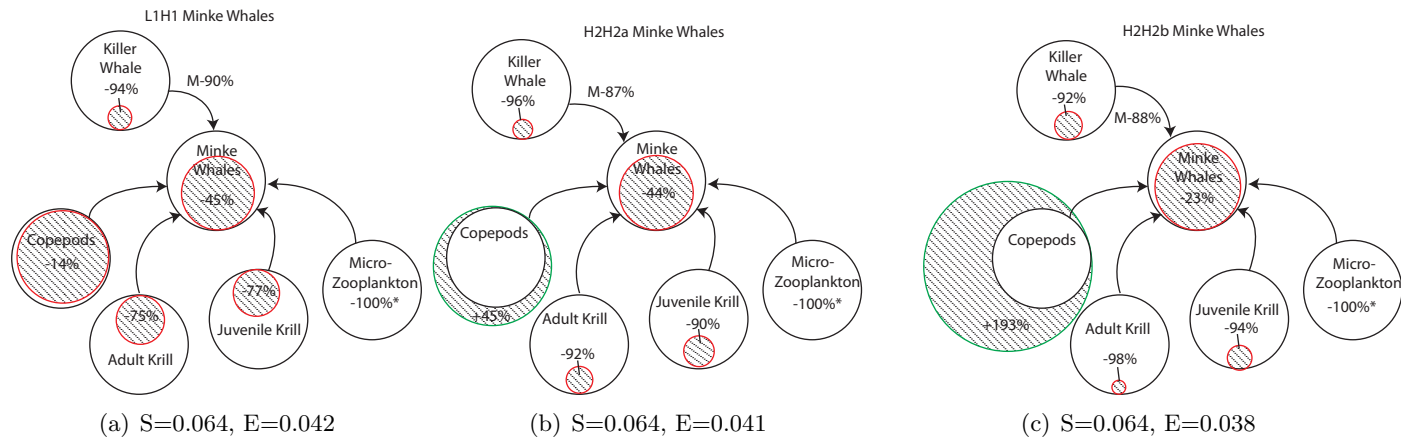


Figure 5.11: Changes in biomass for minke whales with important contributors to diet and mortality. S (mortality at the start of the model 1978) is presented along with E (mortality at the end of the scenario simulation). Ending values for biomass and mortality are averaged over the last 10 years of the simulation. Open circles represent initial biomass for the Ecopath model (1978 value), while the shaded circles represent the ending biomass and are scaled to represent the percent change in biomass from the starting biomass of 100%. *Indicates ending biomass is reduced by 100%.

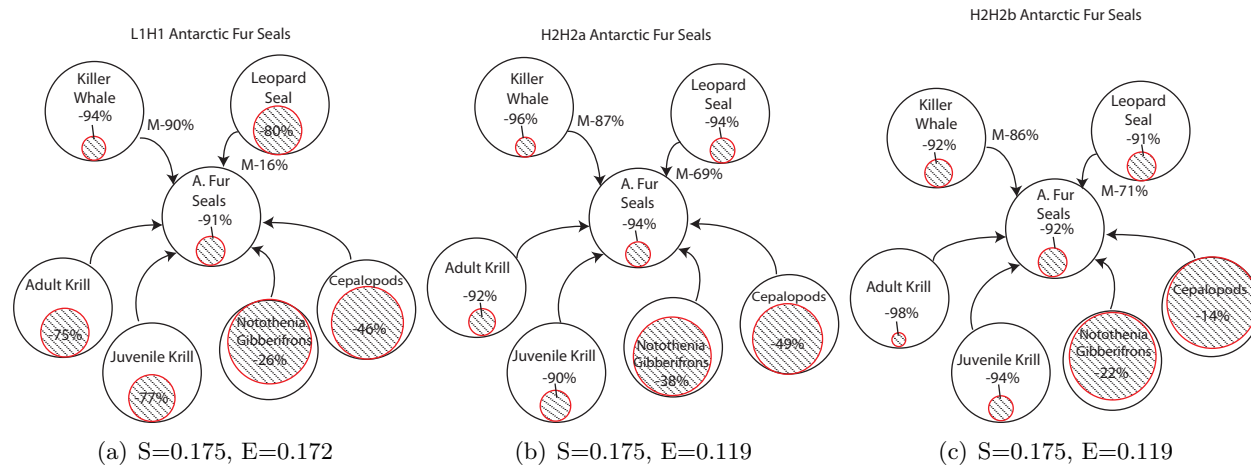


Figure 5.12: Changes in biomass for Antarctic fur seals with important contributors to diet and mortality. S (mortality at the start of the model 1978) is presented along with E (mortality at the end of the scenario simulation). Ending values for biomass and mortality are averaged over the last 10 years of the simulation. Open circles represent initial biomass for the Ecopath model (1978 value), while the shaded circles represent the ending biomass and are scaled to represent the percent change in biomass from the starting biomass of 100%

Other Marine Mammals

Other baleen whales in the model (humpback, blue and fin whales) respond similarly to minke whales for future scenarios. Biomass and mortality decrease (with the exception of fin whale mortality in a few scenarios). Diets that were initially heavily weighted by krill, roughly 70% of the total diets, are replaced by copepods and macro-zooplankton. In most future scenarios copepods contribute over 70% of the diet with macro-zooplankton as the second most abundant prey item for baleen whales. While baleen whales decline in all future scenarios, the H2b harvest scenario results in the least decline for these groups. This can be attributed to the high variability of copepods and the impacts copepods are having on these groups. Crabeater seals, whose diet is heavily based on krill (85% for the Ecopath model), show declines due to a combination of decreased krill in addition to increased mortality. The increased mortality is due to the high starting biomass of this group (relative to other seal species) so as other species decline due to diminished prey availability, there is increased pressure on crabeater seals by leopard seals and killer whales. Both Weddell and Ross seals show patterns similar to the Antarctic fur seal, whereby biomass declines in all scenarios except the L2H2b scenario. Both Weddell and Ross seals have diets based on cephalopods and fish among other items.

Sperm whales and southern elephant seals both have diets based primarily on cephalopods. Declines in both of these groups are greatly impacted by the biomass of the cephalopod group. As top predators, killer whales and leopard seals biomass declines as a reflection of prey items. For killer whales the main prey item, minke whales, continue to be the largest contributor to the diet, even as minke whales decline. Adelie penguins remain the largest contributor to leopard seals diet, although biomass of this group is declining.

5.5 Discussion

Changes in Biomass and Trophic Level

Polar ecosystems are expected to exhibit a net decrease in productivity due to climate change, as reductions in the frequency and magnitude of phytoplankton blooms have been attributed to changes in climate over the last 30 years (Montes-Hugo et al., 2009; Schofield et al., 2010). In addition, Antarctic sea ice losses are estimated to range from 17-31% depending on climate models and CO_2 level increases (Rind et al., 1997; Arrigo and Thomas, 2004). These two factors are responsible for most changes observed in the model. The change in phytoplankton community structure from colder water species (diatoms and ice algae) to warmer water species (cryptophytes and other phytoplankton) through loss of sea ice and increase in SST is responsible for shifting the pathways of nutrients from krill to salps as described by Moline et al. (2000, 2004). There are compounding effects caused by loss of sea ice through mediation functions. The reduction of sea ice increases the vulnerability of larval and juvenile krill to predators while also increasing the foraging area of salps, and further exacerbates the already shifting food web. The implications for krill predators are unfavorable. With this change in producers comes an overall decline in primary production in the model, and a lack of detritus for consumption by benthic organisms, thus reducing the total biomass of the ecosystem.

There is a general trend towards increased ecosystem trophic level in the future, as total production and ecosystem biomass decline. Trophic levels of individual species are generally increasing, as diets are shifting away from lower trophic levels such as producers, to higher trophic levels¹³. Comparisons of pelagic food webs identified species feed at a lower trophic levels in highly productive ecosystems, typically associated with upwelling, while lower production areas showed species feeding at higher trophic levels (Miller et al., 2011). Although Miller et al. (2011) compared more temperate ma-

¹³It should be noted that there were no changes to diet composition from the initial Ecopath model, but rather Ecosim simulations allow predators to feed on a variety of species in simulations as their relative abundance shifts.

rine ecosystems (Japan and California), it was thought the lower TL of the productive ecosystem was due to the increased contribution of zooplankton, primarily euphausiids. TL of the ecosystem increases due to more specialized diets in this study. Comparisons with the Antarctic would fit with the increase in TL of the ecosystem as production decreases and there is a loss of krill in predators diets. In addition, loss of species reduces the omnivory of diets, as proposed by Miller et al. (2011).

Model Uncertainty

Two main factors should be considered with respect to model output. First, the model does not account for changes in physiological limits in species which may cause stress-induced mortality or migration out of the area. Simulations from Cheung et al. (2008) identify distribution shifts of fish species in relation to climate change. *D. mawsoni* distribution becomes restricted in Low climate scenarios, and has the potential to become extinct within 30 years of their model simulation under a High climate scenario due to spatial thermal tolerance¹⁴. Thermal tolerance ranges of species within the model are not accounted for, and will likely cause additional stress for species such as *D. mawsoni*.

Second, immigration of temperate species into Antarctic waters will increase as these thermal ranges shift. Pelagic species are expected to shift their summer and winter ranges due to thermal tolerances (Lam et al., 2008). Climate change is expected to increase the prevalence of invasive alien species (Dukes and Mooney, 1999) which can alter the food web in ways the existing model does not account for. While barriers to the Southern Ocean are more physiological than geographic, increased warming will shift these physiological barriers pole-wards and allow invasions (Aronson et al., 2007). An important thermal barrier for the Antarctic is the Polar front which separates the colder polar water from the warmer temperate water. Movement of this thermal barrier further south would allow for increased immigration of temperate species and should be considered when interpreting model results.

¹⁴Low climate scenario depicted a temperature increase of $0.075^{\circ}\text{C}\cdot\text{y}^{-1}$ at high latitudes, while the High scenario depreciated a $0.15^{\circ}\text{C}\cdot\text{y}^{-1}$ at high latitudes.

There are other impacts of climate change known to effect species that should be considered in the context of individual species results. UV absorbing amino acids are produced in ice algae and act as a built in sunscreen protecting krill from increased UV (Arrigo and Thomas, 2004). The lack of mycosporine-like amino acids or MMAs in krill, will decrease the UV protection of predators as well, potentially increasing mortality. Fish that rely on sea ice for spawning such as *P. antarcticum* are expected to show decreased resistance to UV, through reductions of MMAs in krill, in addition to suffering from loss of ice habitat (Vacchi et al., 2004; Moline et al., 2008).

Changes to Species Groups

Krill declines in the model range from 75-96% for adult and juvenile groups combined. The krill embryo stage demonstrates increases, as in the model this non-feeding stage is not limited by production within the ecosystem. While this is ecologically founded (Marr, 1962; Nicol et al., 1995; Arndt and Swadling, 2006), the implications to the model allow for a higher biomass of the larval krill stage. This increase in lower trophic levels of krill is not long lived, as juvenile krill biomass declines in future scenarios. Declines from 1978-2007 were estimated by the past model (chapter 3) to be 36% from the starting biomass for juvenile and adult groups combined indicating changes in the future will be more extreme for this group. Studies from the southwest Atlantic sector of the Southern Ocean indicate krill density has potentially decreased 80% from 1976 to 2004 (Atkinson et al., 2004; Smetacek and Nicol, 2005). While this compares density from net data and not biomass directly, it verifies that there may have been significant changes to krill populations in the past, and future declines of 75% are not extreme in this context. We consider the implications to the remainder of the food web under the possibility of large scale reductions in krill.

Salp biomass increased in the past model of 32%, while ending biomass for future scenarios resulted in increases ranging from 14-75% depending on scenarios. Salp density was noted as increasing two fold (up to or over two fold) from 1926-2003 (Atkinson et al., 2004). Although the density increase

does not equate to the same changes in biomass, large scale increases are recognized in the data and exhibited by the model presented. As biomass of salps in the model increases, so does the contribution of salps to the diets of predators. Salps are identified to be consumed by a variety of birds, fish and invertebrates (see Pakhomov et al., 2002, for a full list of studies where salps are identified in the diets of predators), and their contribution to the food web increases with biomass. This is acceptable in the model, but the low energetic value of salps should be considered when assessing the potential replacement of krill in predators' diets. Lipid values as % of wet weight for krill (*Euphausia superba*) range from 2.41-6.33 for males and gravid females, while salps (*Salpa thompsoni*) values were 0.1, and copepods ranged from 0.7-9 (Clarke, 1980; Donnelly et al., 1994). Although more recent literature has identified salps to have a higher carbon value than previously described (Ikeda and Bruce, 1986; Dubischar et al., 2006) indicating that although they may have higher energetic values, these values are still lower than reported values for krill and copepods.

The release of copepods from krill, specifically juvenile krill, allows for large increases in biomass especially under the L2H2b and H2H2b scenarios. The implications also transfer to the macro-zooplankton and cephalopod groups resulting in large variations in biomass for this group as well (figures 5.13-5.15). High variance in environmental drivers does not cause such large variations in ending results for harvest scenarios H1 or H2a. These scenarios may elude to an instability of the model, or potentially the ecosystem when high variations in environmental drivers are coupled with removals of the juvenile krill, and should be interpreted cautiously. It should be noted that the removals of juvenile krill in the H2b quota level scenario is larger than all krill stages removed presently (also the H1 harvest scenario). Removals of juvenile krill stages should be an important consideration for future managers.

Model results for myctophids identify this group fares better than others in the future. While this is due to a varied diet in the model, and declines in predators (primarily penguins and birds), other studies support the potential for myctophid success in the future. Moline et al. (2008) noted lanternfish

(myctophid) are not as likely as other species to be impacted by loss of sea ice as their life history has little direct dependence to ice. di Prisco and Verde (2006) also suggest the replacement of ice-associated fish by myctophids as a new food item for higher trophic levels.

Predictions of the future changes to benthos are difficult (Clarke and Crame, 1992). Aronson et al. (2007) suggests the overall biomass of endemic species may be replaced by benthic invaders such as crabs. This would be possible in the future when physiological limitations would diminish as waters warm, as there are no physical barriers preventing invasions. There is the potential that invasions by sub-Antarctic species of benthos and fish would substitute the diets of predators, thus reducing the impacts of declining krill populations.

Declines in Adelie penguins attributed to declines in ice habitat have been established in literature, but it was thought that gentoo and chinstrap penguins were increasing during the same period due to their ability to inhabit warmer areas (Fraser et al., 1992; Fraser, 2006). The model fitted to past data (chapter 3) included immigration rates in an attempt to replicate the Palmer LTER data (Fraser, 2006), but could not account for increases in chinstrap and gentoo penguin biomass. More recent, larger scale studies on penguin populations reveal that these species are declining, with the primary cause being attributed to krill declines (Trivelpiece et al., 2010). Model simulations corroborate the ability of krill declines to explain these declines in all penguin species. There are yet to be any large-scale studies for whales or seal populations to validate model results for these groups. Past studies have indicated declines in predators at S. Georgia due to years of low krill biomass (Hofmann et al., 1998; Brierley and Reid, 1999; Reid and Croxall, 2001), which is the reason for declines in these predators in the model.

Role of Krill in the Ecosystem

Krill are thought to have a pivotal role in Antarctic ecosystems, linking top predators to primary production (Moline et al., 2000, 2004; Smetacek and

Nicol, 2005). Baleen whales migrate from tropical latitudes to feed on krill in summer months (Dawbin, 1966; Tynan, 1998; Murase et al., 2002) indicating their life history is based on krill being available every summer. Model results indicate the potential of krill to be replaced in part by copepods in the ecosystem. Chapter 3 suggested krill may be over-represented in the diets of predators in literature. It is possible within the model to substitute the diets of krill predators with copepods, as predators generally consume both. Energetically, copepods represent a nutritional equivalent to krill with higher lipid concentrations in some cases when comparing gram for gram (Clarke, 1980; Donnelly et al., 1994), more so than salps which also increase in the future. It is unclear whether conditions in the future will actually favor the increase in copepod species, however it may be a consideration for future research.

Future Harvest of Krill

Comparing harvest scenarios, increasing the krill harvest from present day levels to current quota levels further decreases krill biomass in simulations. When comparing the H2a scenario where only adult krill are harvested to the H2b scenario where 25% of the catches are taken from juveniles, there are much larger reductions in biomass for adult and juvenile krill. There are fewer adults being harvested in the H2b scenario, but the targeting of juvenile krill reduces the availability of krill to reach sexual maturity. While these levels were tested based on length-frequency catches of krill and length at maturity (Siegel and Loeb, 1994; Pakhomov, 1995a; Jackowski, 2002), the results should be considered to address the issue that bycatch of smaller krill may be altering adult biomass. Further research into removals of juvenile krill should be addressed in management decisions.

Overall harvest at quota levels does not in itself identify large scale changes in the ecosystem. Krill declines increase from 76% to 94% from the L1L1 to H2H2b scenarios. However, the model does suggest predators will be strained by a lack of krill in the future. Continued harvest of krill will only enhance the stress. While spatial limitations of the fishery or

restriction on temporal overlap may allow for some reprieve to predators, managers will have to prioritize between continued harvest and retaining higher abundances of krill predators in the ecosystem.

Environmental drivers cause higher declines of krill than increased harvest levels. However, as the model is on a temporal scale, spatial overlap will almost certainly compound these effects. Past declines in predators at South Georgia were attributed not only to declines in krill, but also to fisheries operating in close vicinity to predators (Reid and Croxall, 2001). For the past, spatial modeling of the ecosystem may reveal an increased sensitivity to the krill fishery and cause additional impacts for krill predators. In future simulations, the large scale declines in krill may occur faster with spatial overlap of fisheries, but does not identify this as the cause of the declines. Article II of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) addresses the harvest of species (CCAMLR, 1980; Constable et al., 2000). In summary, this article states harvest should be conducted so it: (i) does not decrease any harvested population to levels below those which ensure suitable recruitment, (ii) maintains ecological relationships between harvested, dependent, and related populations, and (iii) prevents changes in the marine ecosystem which are not reversible over two to three decades. Considering the effects to krill by environmental changes alone, managers will have tough decisions to make in the future as expansions of the krill fishery to quota levels will further stress krill populations. Simulations suggest the impacts of the fishery alone may not be great, but it will be taking prey away from higher trophic levels struggling to meet their demands.

5.6 Antarctic Peninsula Biomass and Mortality Figures

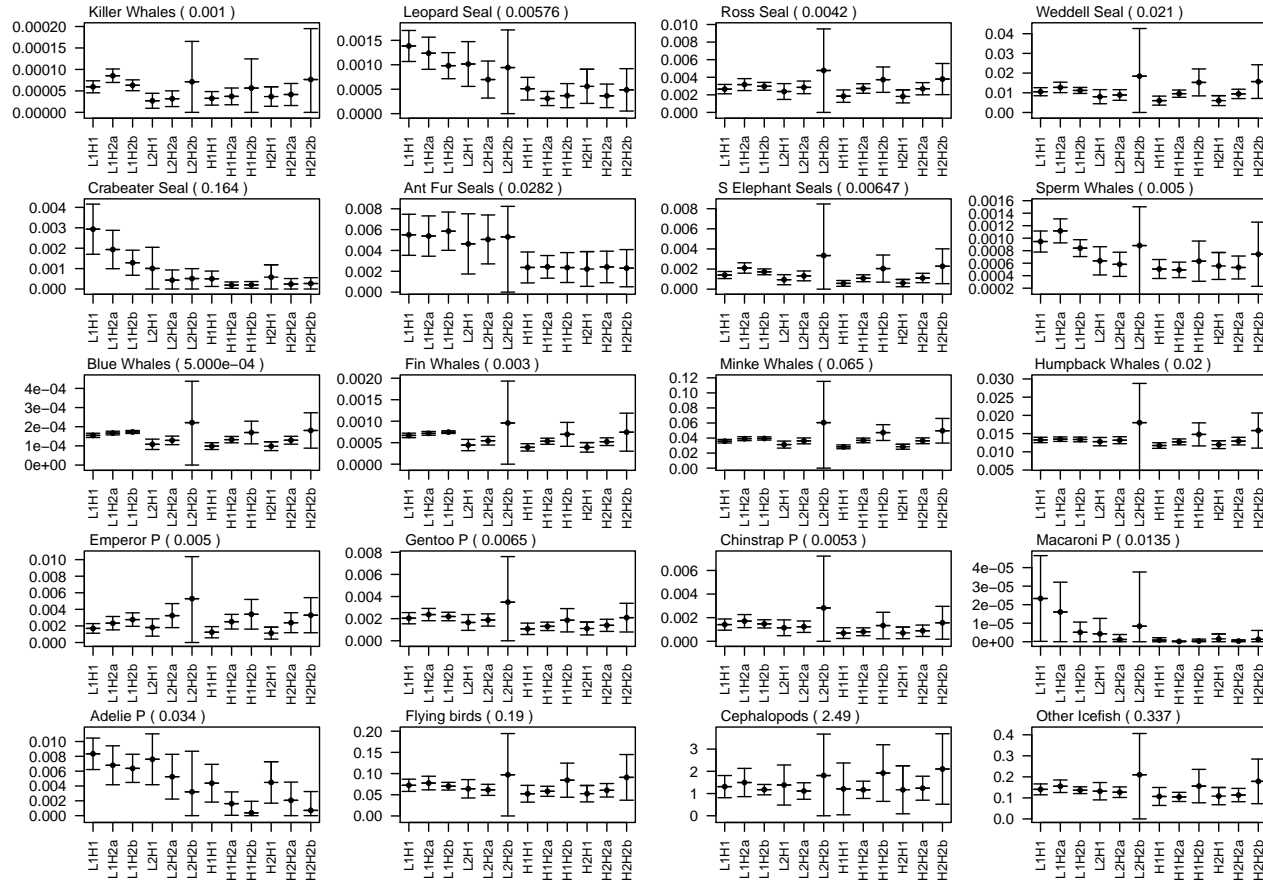


Figure 5.13: Ending biomass by species group for each simulation scenario. Values (in $t \cdot km^{-2}$) represent the mean and 95% CI for the last 10 years of each simulation. Biomass for the first year of simulation is presented above the graph in parentheses for comparison. CI extending into negative values are presented with a minimum biomass of $0t \cdot km^{-2}$

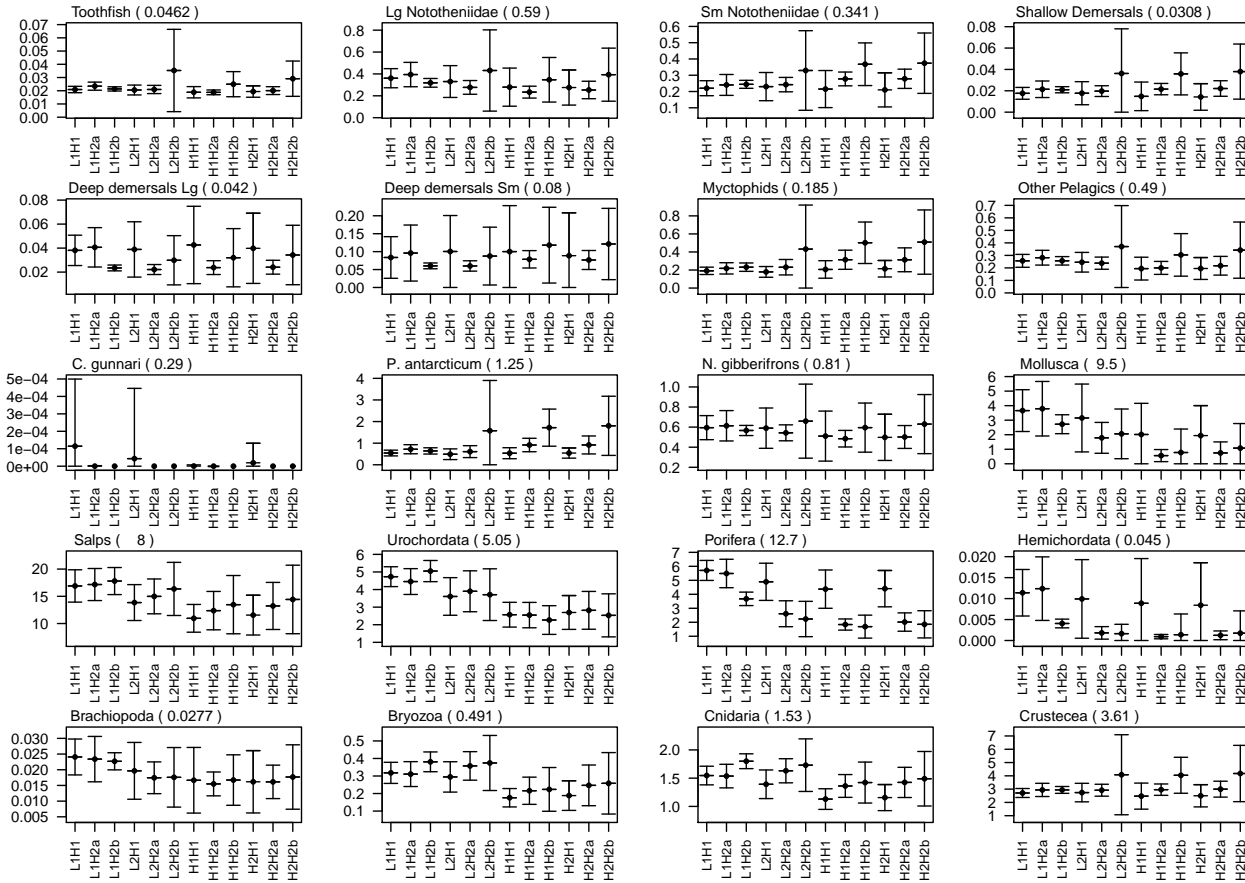


Figure 5.14: Ending biomass by species group for each simulation scenario. Values (in $t \cdot km^{-2}$) represent the mean and 95% CI for the last 10 years of each simulation. Biomass for the first year of simulation is presented above the graph in parentheses for comparison. CI extending into negative values are presented with a minimum biomass of $0t \cdot km^{-2}$

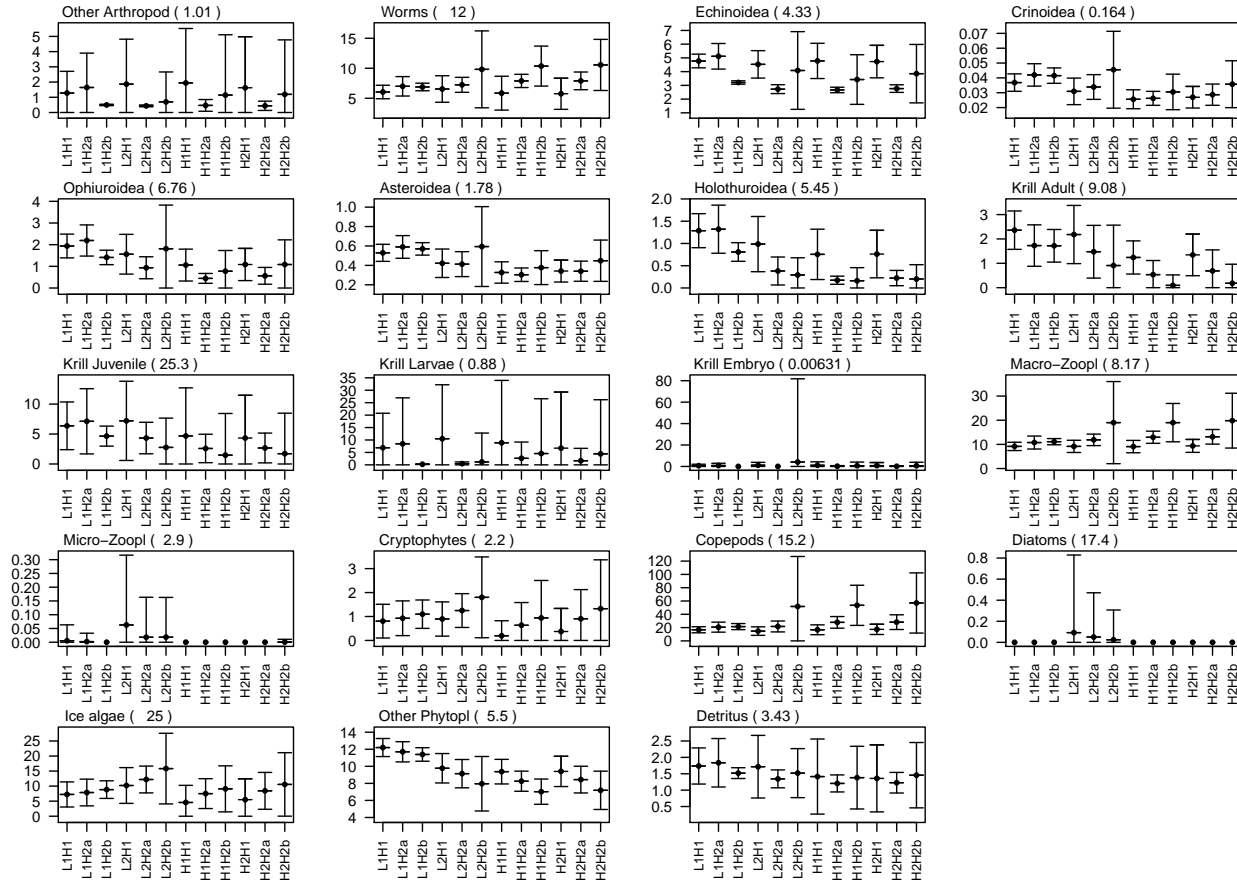


Figure 5.15: Ending biomass by species group for each simulation scenario. Values (in $t \cdot km^{-2}$) represent the mean and 95% CI for the last 10 years of each simulation. Biomass for the first year of simulation is presented above the graph in parentheses for comparison. CI extending into negative values are presented with a minimum biomass of $0t \cdot km^{-2}$

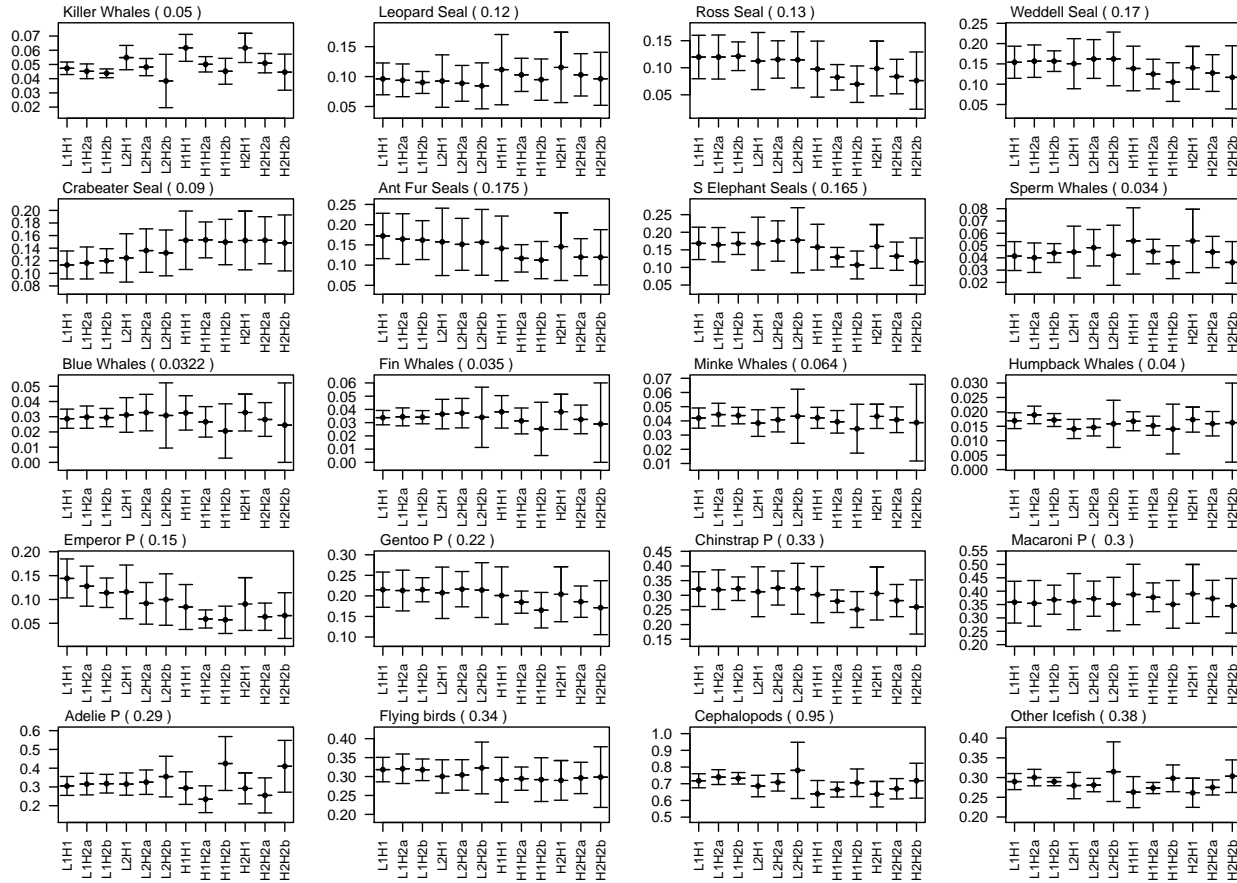


Figure 5.16: Ending mortality (y^{-1}) by species group for each simulation scenario. Values represent the mean and 95% CI for the last 10 years of each simulation. Mortality for the first year of simulation is presented above the graph in parentheses for comparison.

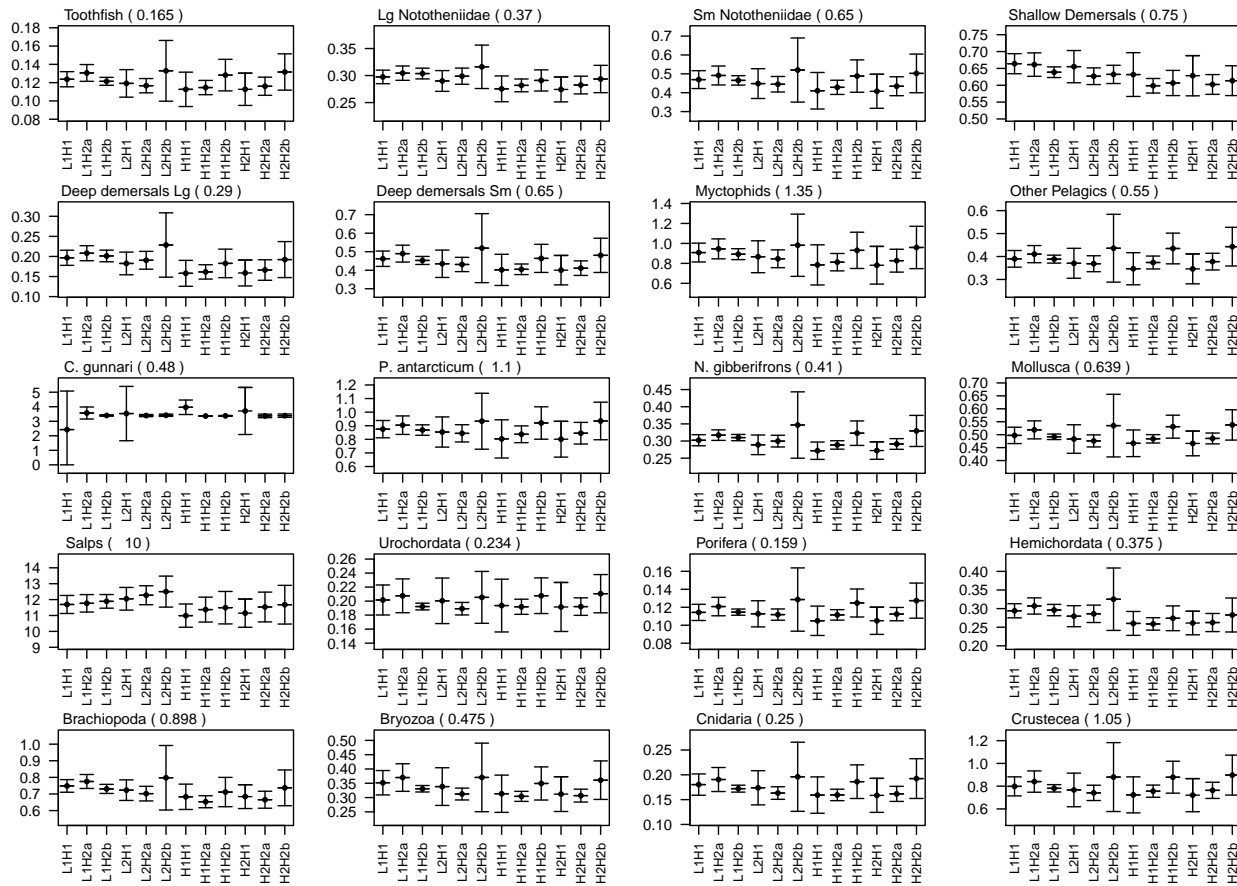


Figure 5.17: Ending mortality (y^{-1}) by species group for each simulation scenario. Values represent the mean and 95% CI for the last 10 years of each simulation. Mortality for the first year of simulation is presented above the graph in parentheses for comparison.

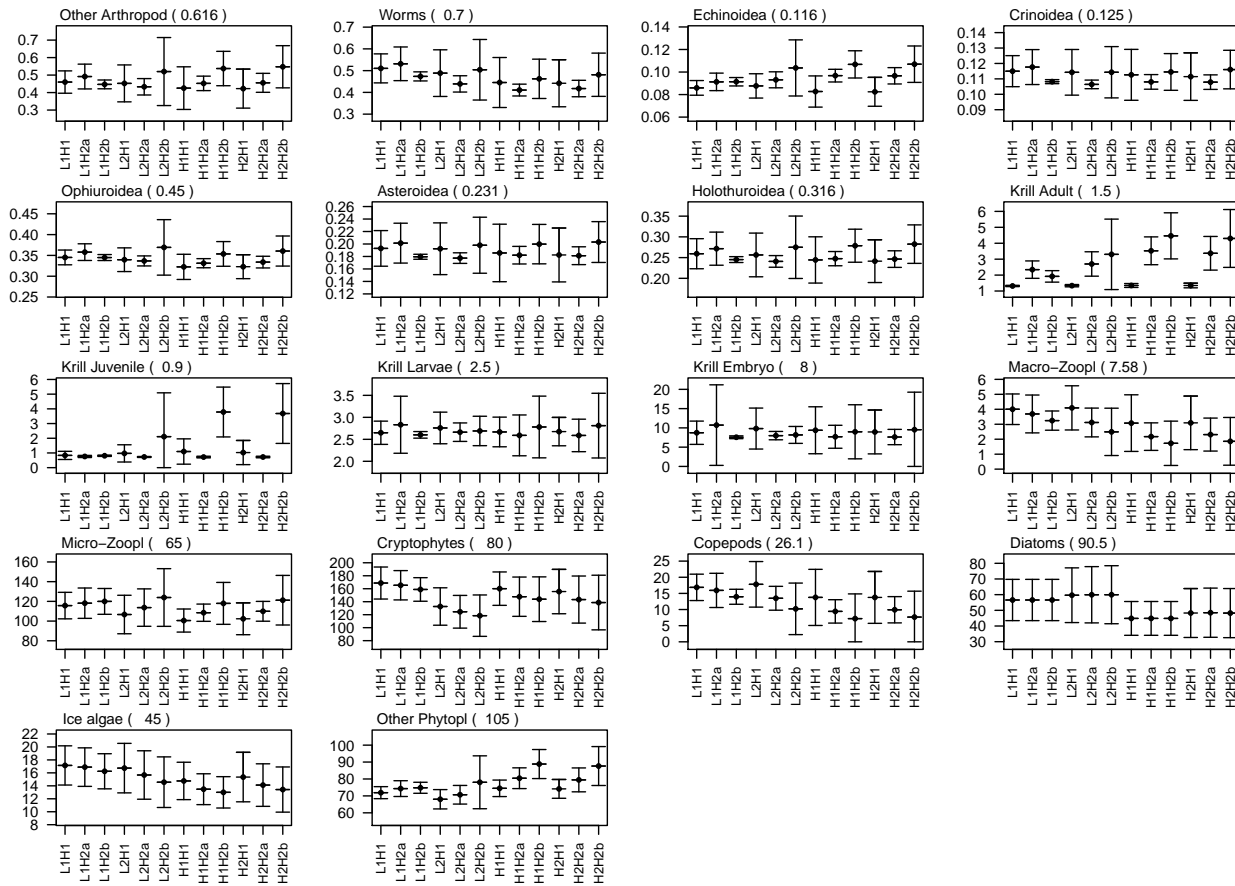


Figure 5.18: Ending mortality (y^{-1}) by species group for each simulation scenario. Values represent the mean and 95% CI for the last 10 years of each simulation. Mortality for the first year of simulation is presented above the graph in parentheses for comparison.

Chapter 6

Estimating the Economic Value of Narwhal and Beluga Hunts in Hudson Bay, Nunavut

6.1 Synopsis

Hunting of narwhal (*Monodon monoceros*) and beluga (*Delphinapterus leucas*) in Hudson Bay is an important activity providing food and income in northern communities, with changes in these species identified in chapters 2 and 4. Despite this importance, there are few studies detailing the economic aspects of these hunts. Here the uses of narwhal and beluga are outlined in addition to estimating revenues, costs and economic use value associated with the hunt, based on harvests for 2007. Incorporation of cost sharing and including an opportunity cost of labour is explored as it influences model outputs. The economic use value for the communities participating in each hunt averaged a negative value of \$9399 for beluga and a positive value of \$133,278 for narwhal in 2007. When broken down on a per capita basis this yielded mean estimated values of \$44 and -\$1 for narwhal and beluga respectively. Including the effects of cost sharing with one other hunting activity resulted in increasing the value to \$266,504 for beluga and \$321,500 for narwhal. Narwhals provide a higher value per whale, in addition to a higher per capita total economic value to the community as resources are shared among fewer communities compared to belugas. However, the beluga

hunt overall provides greater revenue, as more belugas are harvested. Our results indicate that the value of whales to communities is largely due to their food value, in keeping with literature on other hunting activities in the Arctic.

6.2 Introduction

Subsistence whaling in the Canadian Arctic has been an important activity for native communities, with hunts being culturally significant (Stewart and Lockhart, 2005; Nuttall, 2005). Increasing human populations, combined with declines in marine mammal populations in Hudson Bay, reveal the importance of hunting to this region. Hunting and the use of 'country foods' (i.e., foods hunted and gathered from the land), are considered an important aspect to life in northern communities, and contribute to reinforcing social and cultural relationships (Nuttall, 2005). Not only does hunting provide a source of protein for people, Inuit have reported a lack of resistance to illness when not consuming country foods (Freeman, 2005). In Hudson Bay (figure 6.1), Inuit culture has been strongly linked to marine species throughout history (Stewart and Lockhart, 2005). They have traditionally hunted a variety of species, including bowhead, beluga, narwhal, polar bears, walrus, seals, fish and birds.

The importance of northern species to Arctic communities has been recognized and studied for several years. The state of Alaska had included subsistence hunting as an economic sector in their studies of ecosystem importance (Colt, 2001). The subsistence value of moose in Alaska has also been analyzed (Northern Economics Inc, 2006). Comprehensive assessments of polar bear hunting at various communities in the Canadian Arctic assigned economic values to traditional and sport hunts and includes different perspectives on hunting activities (Freeman and Foote, 2009). Analysis of seal hunting in Canada (Wenzel, 1991) also explored cultural and economic factors involved in hunting. Loring (1996) provided a summary of all summer hunting activities near Igloolik (a community north of Hudson Bay in Nunavut) in 1992, assigning an economic value of \$6 million to all hunt-

ing activities for that year. Research on narwhal and beluga harvest has focused on specific aspects of individual hunts, such as technical aspects of hunting in general (Weaver and Walker, 1988), and the economic importance of ivory from narwhals (Reeves, 1992a), rather than comprehensive analyses. Unfortunately, such studies are not available for all species or communities involved in hunting. In this paper, we aim to provide an assessment of the economic factors involved in the hunting of two important whale species: beluga and narwhal, in communities in Nunavut, Canada.

Community populations in Nunavut (one of Canada's northern territories) are projected to increase from 32,416 in 2010 to 44,581 in 2036 (Nunavut Bureau of Statistics, 2010), which has the potential to increase pressure on marine mammal stocks in the area. While catches of beluga have remained relatively stable since the 1980s, narwhal catches increased in the late 1990s and remained at a higher level (DFO, 1990, 1991, 1992, 1993, 1994, 1995, 1996, 1997; Stewart and Lockhart, 2005; JCNB/NAMMCO, 2009). Furthermore, estimates of the 2008 northern Hudson Bay narwhal stock have indicated the possibility of declines up to 50% of previous estimates from 1984 and 2000 (DFO, 2010a), suggesting stock decline although survey results were not conclusive. The 2008 survey noted poor weather conditions, and the population was potentially underestimated in the survey (DFO, 2010a), a 2011 survey is still awaiting results. In December 2010, the Canadian government implemented a ban the export of tusks from the northern Hudson Bay narwhal population, requiring them to remain in Canada, and recommended that CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) implement a ban on the export of these narwhal tusks from communities hunting the northern Hudson Bay population of narwhals (DFO, 2010b). While this does not affect the quotas on the number of whales that can be harvested, it will ultimately impact the economic value of the narwhal hunt, by limiting the export of narwhal tusks from these communities to within Canada. Communities are currently considering legal options for potential lost revenue. In addition to lost economic potential, the impact of climate change and of harvesting and trade limitations on the culture of northern communities could be largely

negative (Nuttall, 2005).

Of the three beluga stocks hunted within Hudson Bay, the eastern Hudson Bay population has declined in the past but has not shown a recovery, and has been listed as endangered by COSEWIC (Committee on the Status of Endangered Wildlife in Canada) (NAMMCO, 2005a), while still enduring hunting pressure. Species distributions of narwhal and beluga are expected to contract poleward as a result of climate change, with negative impacts to hunters (Hovelsrud et al., 2008). Hudson Bay has already shown shifts in seasonal ice cover (Gagnon and Gough, 2005), and due to its southerly location will likely be one of the first areas negatively affected by competing species, new predators, disease, and a change in available food.

This paper presents the different aspects of the narwhal and beluga subsistence hunts in the Hudson Bay region, along with the economic ramifications to the local communities. While commercial whaling was once important both nationally and regionally, it no longer exists in Canada. Thus, in the context of this paper, hunting and whaling are limited to subsistence hunting. Beluga and narwhal were chosen for the focus of this study as they are hunted annually, and landings are recorded. Analysis was limited to the Nunavut portion of Hudson Bay (figure 6.1), as part of an International Polar Year initiative focusing on Hudson Bay, and have based the model on knowledge of communities within the Nunavut side due to knowledge of the region. For each hunt, revenue, cost and net economic value are estimated for 2007. For the purposes of this paper, use value is presented and refers to economic value hereafter. Our aim is to help facilitate a better understanding of the contributions each hunt brings to the communities discussed, in order to provide baseline information in the event of changes in future hunting patterns. Future geographic expansion of the model for additional Nunavut and Nunavik communities is ideal, but beyond the scope of this project. An Arctic wide assessment acknowledged recent harvesting studies are evaluations on the current knowledge, and are still within the early stages of development (Nuttall, 2005). While this paper aims to be useful in the context of current events, the model presented is a first step aiming to provide an overview of hunting economics, yet further research is needed

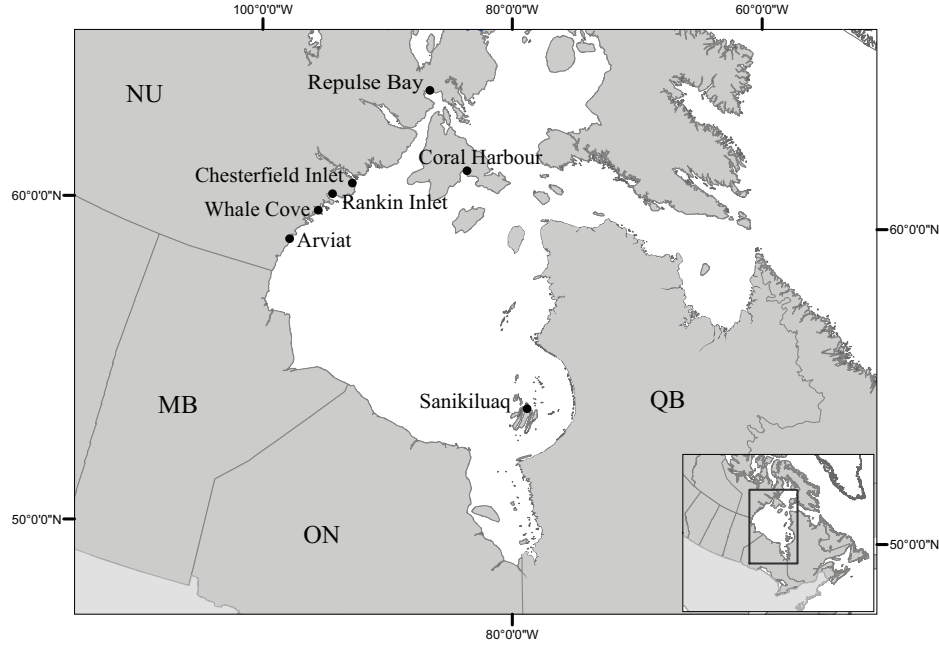


Figure 6.1: Map of communities in Nunavut portion of Hudson Bay hunting narwhal or beluga. Nunavik, Ontario, and Manitoba communities are not shown.

to help develop a more comprehensive economic picture.

6.3 Methods

Using published and unpublished data combined with values provided by field researchers, we developed an economic model to estimate the total use value for beluga and narwhal hunts for the 2007 year. For this analysis, total use value was calculated using Monte Carlo simulations whereby parameters for each equation are selected randomly from an assigned distribution to calculate total use value. This is repeated for 10,000 iterations to generate a distribution of values for costs, revenues, total use value and per capita use value. Ranges for input parameters were assigned a uniform distribution to account for uncertainty. Data for catches were taken from 2007, the

6.3. Methods

most recent year data were published on both narwhal and beluga catches (JCNB/NAMMCO, 2009), with most communities harvesting at or near their quota limit. We present this model as an estimate of economic costs and revenues based on the best available data and assumptions by researcher, but recognize the need for improved estimates in the future, as data sets become richer.

Information on hunting activities was taken from published literature where available. Authors provided some estimates, in addition to collaborators involved in biological sampling and observation of both the narwhal and beluga hunts in the communities discussed. Specific prices and costs for individual factors (fuel, meat replacement, narwhal tusk value, carving values) were obtained in 2008 from Repulse Bay. These values were used as representative of costs and prices in other Hudson Bay communities.

Carvings (narwhal and beluga) and narwhal tusks are primarily sold to the local Co-op, a locally-owned and democratically-operated northern business that operates as part of a larger network of 31 community-based business enterprises located throughout Nunavut and the Northwest Territories (Arctic Co-operatives Limited). Each independent Co-op purchases carvings from local artists, and Arctic Co-operatives Limited markets Inuit art on both a retail and wholesale basis, with carvings sold to art dealers, distributors, and the general public (<http://www.arcticco-op.com/index.htm>). Some hunters may sell carvings or tusks to travelers directly, for a higher price than the Co-op would pay. Prices of tusks and carvings used were based on the value a hunter/carver would receive for selling the piece to the Co-op. Carvings are then generally sold to art dealers, distributors, or the general public resulting in higher prices. A portion of the additional revenue is redirected back into the Co-op, or other community programs. However, as these added values that are generated are not available, values for carvings and tusks was calculated using the price carvers are paid when selling items to the Co-op. Costs were first calculated under the assumption that the opportunity cost to hunt was zero. This assumption was then relaxed and costs were re-assessed including an opportunity cost function.

Revenues and costs are calculated for the entire hunt and on a per capita

basis. We chose these approaches for two reasons. First, to identify the scope of the use value for both hunts. Second, because in a subsistence economy resources are shared among community members and are an important value of Inuit culture (Wenzel, 2009b,a), we also calculate the per capita use value. All values are presented in Canadian dollars.

Beluga

Belugas begin their annual migration into Hudson Bay in the springtime, from Hudson Strait down the eastern and western coasts of Hudson Bay to their summering locations in eastern Hudson Bay, western Hudson Bay, and James Bay (DFO, 2001). Belugas hunted during these migration routes are utilized for the muktaaq (or thin layer of blubber with the skin attached), with a small portion of the meat consumed or traditionally fed to dogs (Tyrrell, 2007). Communities in Hudson Bay generally do not consume large portions of muscle protein, although other Arctic communities often dry the meat and store for later consumption (J. Orr, pers. comm., 2010). While non-indigenous people may consider this to be wasteful, to Inuit culture a partially-flensed whale is not wasteful. Rather the remaining edible tissues and meat will be consumed by other animals (Freeman, 2005). Teeth and bones, more specifically, vertebrae, are used for carvings, with bones being dried in the sun for carving at a later date.

Beluga Catch

The 2007 beluga catch, N_B , was set to 180 whales for 2007, based on reported catch data (JCNB/NAMMCO, 2009). This included catches from the following communities (number of whales harvested): Arviat (50); Chesterfield Inlet (12); Coral Harbour (7); Rankin Inlet (38); Repulse Bay (21); Sanikiluaq (52), and Whale Cove (10). Catches for Sanikiluaq were not available for 2007 so a five year average from 2002-2006 was used as the 2007 catch in these communities.

Beluga Revenue

The revenue from the beluga hunt is the sum of the value of the meat obtained from the muktaaq, along with other edible portions of the whale, in addition to the income from the vertebrae and teeth, which are turned into carvings. The total revenue of beluga whales, TR_B , is calculated for all the whales harvested as:

$$TR_B = R_{Bm} + R_{Bc} \quad (6.1)$$

where R_{Bm} is the value of the meat, for which we essentially use the cost of replacing meat from the beluga whale with store-bought protein sources, and the revenue from beluga carvings, R_{Bc} . This replacement value of meat, R_{Bm} , is further broken into:

$$R_{Bm} = N_B * w_B * e_B * c_{pB} \quad (6.2)$$

where w_B is the weight of an individual whale, e_B is the edible portion of the beluga, and c_{pB} is the replacement cost of other protein sources from the local store.

The revenue from beluga carvings is estimated as:

$$R_{Bc} = N_B * [(T_B * P_{Bt}) + (V_B * P_{Bv})] \quad (6.3)$$

where T_B is the number of teeth per beluga used for carvings, V_B is the number of vertebrae per beluga used for carvings, and P_{Bt} and P_{Bv} are the prices of carvings from one tooth or vertebrae, respectively.

Beluga Cost

The cost of the beluga hunt is calculated for all communities combined (Arviat, Chesterfield Inlet, Rankin Inlet, Repulse Bay, Sanikiluaq, and Whale Cove). Baker Lake was excluded from the model as there was only one year of reported hunts from 1977-2007 (JCNB/NAMMCO, 2009). Costs here include both variable (i.e., bullets and fuel) and fixed costs (i.e., rifles and

6.3. Methods

boats). Within the fixed cost estimate a term for depreciation is included. Costs are calculated on a per trip basis, with the number of beluga hunting trips, B_{trip} , dependent on the number of hunters, M_B , the number of trips each individual takes, I_B , and the size of the hunting group, B_{gr} :

$$B_{trip} = \frac{M_B * I_B}{B_{gr}} \quad (6.4)$$

The per trip costs of the beluga hunt are broken into the cost of boats, C_{Bb} , the cost of guns, C_{Bg} , the cost of fuel, C_{Bgs} , and the cost of bullets, C_{Bbu} . The cost of all boats per trip, C_{Bb} , is estimated as:

$$C_{Bb} = \frac{N_{bo} * (c_{bo}/T_{bo})}{B_{trip}} \quad (6.5)$$

where N_{bo} , the number of boats, is represented as M_B/B_{gr} . The parameter c_{bo} is the cost of one boat, with a replacement time, T_{bo} . The cost of all guns per beluga trip, C_{Bg} , assuming each hunter has 1 gun, is estimated as:

$$C_{Bg} = C_R * \frac{M_B * c_{gu}/T_{gun}}{B_{trip}} \quad (6.6)$$

With c_{gu} as the cost of one gun, T_{gu} as the replacement time of a gun, and C_R as the percentage of hunters participating in the Canadian Ranger program. Canadian Rangers are a component of the Canadian Forces and are responsible for surveillance, patrolling, reporting activities, and collecting data <http://www.army.forces.gc.ca/land-terre/cr-rc/crpg-gprc-eng.asp>. This program subsidizes hunters by providing guns, which is further explained in Section 2.5. The cost of bullets per trip, C_{Bbu} , is estimated as:

$$C_{Bbu} = C_R * \frac{bu * M_B * I_B * c_{bu}}{B_{trip}} \quad (6.7)$$

where the total number of bullets used is dependent on the number of men hunting, M_B , the number of trips each hunter takes, I_B , the number of bullets used per hunter, bu , and the cost of each bullet, c_{bu} . The cost of fuel

per beluga hunting trip, C_{Bgs} , is estimated as:

$$C_{Bgs} = L * c_{gs} \quad (6.8)$$

where L is the liters of fuel used per trip, and c_{gs} is the cost of fuel per liter. The total cost for hunting beluga over all trips, TC_B , is the sum over the costs for the boat, guns, bullets and fuel:

$$TC_B = B_{trips} * (C_{Bb} + C_{Bg} + C_{Bbu} + C_{Bgs}) \quad (6.9)$$

Beluga Total Use Value

The total use value from the beluga hunt, Π_B , is calculated as the difference between the total revenue and total cost:

$$\Pi_B = TR_B - TC_B \quad (6.10)$$

We also computed this value on a per capita basis, π_B , estimating the value of the hunt to every member of the community, based on the population size B_{pop} .

$$\pi_B = \frac{\Pi_B}{B_{pop}} \quad (6.11)$$

Narwhal

The narwhal hunted in Hudson Bay are part of the northern Hudson Bay stock. Historically, this population was believed to be part of the larger Baffin Bay narwhal population. However, recent studies indicate that, although winter ranges have the potential to overlap, Hudson Bay narwhal show summer site fidelity near Southhampton Island and Repulse Bay (COSEWIC, 2004a; Westdal et al., 2010). Narwhal leave their winter range to begin migration to their summer location near Repulse Bay around May and stay until the beginning of September (Westdal et al., 2010). The narwhal hunt in Repulse Bay generally starts after the ice breaks up in mid June, and continues until August when the whales leave the area (Freeman et al., 1998). 2007 was a year of unprecedented decline in sea ice, allowing the quota to be

reached easily as narwhal were able to come close to shore (Cressey, 2007; Greer, 2007). During years of high sea ice, narwhal are hunted from the ice edge using snowmobiles, but after the ice is gone they are hunted from the open water using boats (Weaver and Walker, 1988). Snowmobiles were not included in this analysis for narwhal due to 2007 being a low ice year and boats as the primary tool for harvest of narwhals in Hudson Bay (DFO, 1998; Greer, 2007).

Narwhal have traditionally been hunted for muktaaq, which is highly prized in native communities (Hrynyshyn, 2004; Freeman, 2005). In addition, tusks from the male narwhals are sold to the local Co-op, where they are picked up by art dealers to be sold in other locations. While females generally remain functionally toothless throughout life, a small percentage do grow a full length tusk. Additionally, there have been reports of males with two erupted tusks, however it has been estimated that these are rare cases occurring in less than 1% of the population (Reeves, 1992a), and therefore this possibility was not incorporated into the model. Teeth and bones from both males and females are used for carvings and are sold to local tourists, or to the Co-op for further distribution.

Narwhal Catch

Narwhals are typically hunted at 3 Hudson Bay communities: Repulse Bay, Rankin Inlet, and Whale Cove, with most, if not all, of the catches in most recent years from Repulse Bay. For 2007, the total catch, N_N , was reported as 81 whales: 9 whales from Rankin Inlet, 72 whales from Repulse Bay, and none from Whale Cove (JCNB/NAMMCO, 2009). As male narwhals have a higher value, due to their tusks, catches were split into male, N_M , and female, N_F , whales. Of the 72 whales reported from Repulse Bay in 2007, 41 were male (DFO unpublished data). The male catches from Repulse (56%) were assumed to also be representative of Rankin Inlet for 2007.

Narwhal Revenue

Total revenue of narwhal, TR_N , is calculated following the same method as beluga for two separate uses: consumption in the form of narwhal meat, plus the revenue from narwhals in the form of carvings.

$$TR_N = R_{Nm} + R_{Fc} + R_{Mc} \quad (6.12)$$

where R_{Nm} is the revenue from narwhal meat (males and females), R_{Fc} is the revenue from female carvings, and R_{Mc} is the revenue from male carvings, due to differences in revenue caused by male narwhal tusks. The revenue from the meat is calculated as the replacement cost of protein:

$$R_{Nm} = [(N_F * w_{NF}) + (N_M * w_{NM})] * e_N * c_{pN} \quad (6.13)$$

With w_{NF} and w_{NM} as the weights of female and male narwhal respectively. The edible portion of narwhals, e_N , and c_{pN} is the cost of meat replacement per kg of narwhal meat. The revenue from the female carvings R_{Fc} , which is comprised of incisor teeth and vertebrae is equal to:

$$R_{Fc} = N_F[(F_{to} * P_{to}) + (V_N * P_{NV})] \quad (6.14)$$

where F_{to} is the number of incisor teeth used for carvings for females, P_{to} denotes the price of the carvings made from teeth, V_N , is the number of vertebrae used per whale, and P_{NV} is the price for a carving made from a vertebrae. Prices of carvings for teeth and vertebrae, in addition to the number of vertebrae used per whale were the same for male narwhals. For males the revenue is split into revenue from vertebrae and teeth, R_{Mvt} , and revenue from tusks, R_{Mtu} . Revenue from the male vertebrae and teeth was set to:

$$R_{Mvt} = N_M * [(M_{to} * P_{to}) + (V_N * P_{NV})] \quad (6.15)$$

using the same prices for carvings and teeth as females. M_{to} is the number of teeth used for carvings from male narwhal.

Revenue from male tusks is estimated as:

$$R_{Mtu} = N_M * [(T_w * L_{tu} * P_{wt}) + (T_c * L_{tu} * P_{ct})] \quad (6.16)$$

where T_w is the percentage of tusks sold whole with the price of whole tusks, P_{tu} , and T_c is the percentage of tusks turned into carvings, set to $(1-T_w)$, with the price of tusk carving, P_{ct} . It should be noted that both prices are dependent on the length of the tusk, L_{tu} .

Narwhal Cost

The narwhal total cost, TC_N , is calculated for the communities of Repulse Bay and Ranklin Inlet, using the same basic equations as the beluga hunt, with the same ranges associated to costs of boats, guns, and bullets, in addition to replacement times. Costs are calculated on a per trip basis, with the number of narwhal hunting trips, N_{trip} , estimated as:

$$N_{trip} = \frac{M_N * I_N}{N_{gr}} \quad (6.17)$$

where M_N is the number of narwhal hunters in the two communities, I_N is the number of individual trips each hunter takes, and N_{gr} is the size of narwhal hunting groups.

Costs for individual boats, guns, and bullets, (c_{bo} , c_{gu} , and c_{bu}) used the same values as the beluga hunt. Replacement times for boats and guns, (T_{bo} and T_{gu}) also used the same values. The per trip cost of boats hunting narwhal, C_{Nb} , is estimated as:

$$C_{Nb} = \frac{N_{Nb} * (c_{bo}/T_{bo})}{N_{trip}} \quad (6.18)$$

with the number of boats for narwhals, N_{Nb} , depending on the number of hunters and the size of hunting groups (M_N/N_{gr}). The cost of guns per narwhal trip, C_{Ng} , is calculated assuming each hunter has one gun:

$$C_{Ng} = C_R * \frac{M_N * c_{gu}/T_{gu}}{N_{tr}} \quad (6.19)$$

The cost of bullets per trip:

$$C_{Nbu} = C_R * \frac{bu * M_N * I_N * c_{bu}}{N_{trip}} \quad (6.20)$$

used the same cost per bullet, c_{bu} , as beluga hunting. Finally the cost of fuel used per narwhal trip, C_{Ngs} , was set to:

$$C_{Ngs} = L * c_{gs} \quad (6.21)$$

with the liters of fuel used per trip, L , and cost of fuel per liter, c_{gs} . The total cost of narwhal hunting, TC_N , is therefore calculated as the sum of all cost components: boats, guns, bullets and fuel:

$$TC_N = N_{tr} * (C_{nb} + C_{Ngu} + C_{Nbu} + C_{ngs}) \quad (6.22)$$

Narwhal Total Use Value

The total use value for narwhals, Π_N , is calculated as the difference between the total revenue and total cost of the hunt:

$$\Pi_N = TR_N - TC_N \quad (6.23)$$

with the per capita value, π , calculated as:

$$\pi_N = \frac{\Pi_N}{N_{pop}} \quad (6.24)$$

where the population size of narwhal hunting communities, N_{Pop} .

Opportunity Cost

In the above cost functions, we assumed that the opportunity cost of labour, essentially what the hunter must forgo in order to hunt, is equal to zero. This assumption was based on anecdotal evidence from other hunts such as polar bear hunting in Clyde River where Inuit commented on working casual employment to cover the costs of hunting supplies before quitting to go hunting

(Wenzel, 1991). Other researchers have commented on the perception that hunters prefer hunting to alternative employment, even taking vacation time or missing work to hunt (B. Dunn and J. Orr pers. comm 2010). Jobs in some northern communities can be hard to obtain (Loring, 1996). Economic assessments have in the past assigned a wage to hours worked to calculate the opportunity cost of hunting such as Foote and Wenzel (2009) who used an opportunity cost of \$12 an hour for polar bear hunting in Clyde River.

A sensitivity analysis was performed on the opportunity cost of hunting to identify how our assumption of opportunity cost equal to zero affected total cost and economic use value. Here, we calculate the opportunity cost per community based on the average income and the time spent hunting. To do this, the median income for persons over 15 (In), is multiplied the ratio of the number of employed people in the community (N_{em}), to the total number of people in each community in the work force (employed and unemployed) (N_{lf}) to give an average income per employable community member. This value was then multiplied by the number of hunters N_{hun} and number of days spent hunting (D_{hun}). OC per community is thus calculated as:

$$OC = In * \frac{N_{em}}{N_{lf}} * N_{hun} * D_{hun} \quad (6.25)$$

Income and employment numbers were obtained from census data of each community (Statistics Canada, 2006). The number of hunters is either M_B or M_N for the beluga and narwhal hunt respectively, while the number of days spent hunting each year is equal to the number of trips per hunter (I_B or I_N for beluga and narwhal hunts respectively). Opportunity cost for communities hunting both narwhal and beluga are calculated separately for each hunt.

Cost Sharing

Use values for beluga and narwhal hunting activities are calculated under the assumption that all costs are incurred for each hunting activity independently. For example, that hunters purchase a boat and a gun specifically for the purpose of hunting beluga or narwhal. Rankin Inlet is a community

which hunts both narwhal and beluga, in addition to other species. It is almost certain that, in this community, gear is used for both hunts, therefore reducing the costs associated with each individual hunt. For all communities, the cost of hunting whales is re-assessed with the new assumption that costs are shared with other hunting activities, as boats, guns, and fuel may be used to hunt a variety of species (whales, seals and birds) on the same trip. While there are some trips which are intended to hunt beluga or narwhal exclusively, this was considered a rarity rather than the norm, occurring more frequently for narwhal hunts which have a shorter season than beluga. Given this cost-sharing possibility, we reassessed the cost of hunting according to the number of other hunting activities hunters are likely to participate in throughout the year. Costs for boats, guns, and fuel were shared, however costs for bullets remained the same as they can only be used once.

Model Inputs

Parameter values used for model inputs are summarized in table 6.1. Catch statistics for both hunts were used as single estimates rather than ranges, as data were provided (JCNB/NAMMCO, 2009). Proportions of male vs. female narwhals were provided from catch records through DFO (DFO unpublished data) for Repulse Bay where a majority of narwhal are caught. The same proportion of male to female narwhals was applied to catches from Rankin Inlet.

Table 6.1: Parameters inputs for model equation.

Parameter	Lower Range	Upper Range	Description	References
N_B	180	180	# Beluga	(JCNB/NAMMCO, 2009; NAMMCO, 2005a)
w_B	600	1,100	Weight of beluga (Kg)	(Brodie, 1971)
e_B	5	25	Edible portion of Beluga (% Body weight)	(Reeves, 1992b; Ashley, 2002; Hrynshyn, 2004; Tyrrell, 2007)
c_{pB}	6.9	39	Replacement cost of meat (\$ per Kg)	† ¹
T_B	0	2	Teeth per beluga	‡
V_B	0	2	Vertebrae per beluga	‡
P_t	20	200	Price of carving for 1 tooth(\$)	†
P_v	60	250	Price of carving for 1 vertebrae(\$)	†
M_B	10	40	# of beluga hunters (% of community)	‡
B_{pop}	7,364	7,364	Population of all beluga communities	(Statistics Canada, 2006)
B_{gr}	1	5	Beluga hunting group size	‡
I_B	10	15	Trips per beluga hunter (# trips/year)	‡
c_{bo}	3,000	20,000	Cost of boat (\$)	‡
N_N	81	81	# Narwhal	(JCNB/NAMMCO, 2009)
N_f	35	35	# Female Narwhals	(DFO unpublished data)
N_m	46	46	# Male Narwhals	(DFO unpublished data)
w_{NF}	800	1,000	Weight of female narwhal (kg)	(Garde et al., 2007)
w_{NM}	1,500	1,800	Weight of male narwhal (kg)	(Garde et al., 2007)
e_N	5	25	Edible portion of Narwhal (% Body weight)	(Reeves, 1992b; Wenzel, 1991; Ashley, 2002; Wenzel, 2009b)
c_{pN}	6.9	39	Replacement cost of meat (\$ per Kg)	† ¹
F_{to}	0	2	Teeth per female Narwhal	‡
M_{to}	0	1	Teeth per male Narwhal	‡
V_N	0	2	Vertebrae per narwhal	‡
Continued on Next Page				

Table 6.1 Continued				
Parameter	Lower Range	Upper Range	Description	References
L_{tu}	2.5	8	Length of tusks (feet)	(Weaver and Walker, 1988; Garde et al., 2007; Reeves, 1992a)
T_w	95	100	% of tusks sold whole	(CITES, 2004)
R_{wt}	100	180	Revenue from whole tusk per foot (\$)	†
P_{ct}	60	200	Price of tusk carving per foot (\$)	†
M_N	20	50	# of Narwhal hunters (% of community)	(Greer, 2007)‡
N_{gr}	1	5	Narwhal hunting group size	(Greer, 2007; Sloan, 2008)‡
N_{pop}	3,459	3,459	Population of narwhal communities	(Statistics Canada, 2006)
I_N	5	10	Trips per narwhal hunter (# trips/year)	‡
T_{bo}	4	10	Boat replacement time (years)	(Wenzel, 1991)‡
c_{gu}	700	1,200	Cost of gun (\$)	(www.cabelas.ca)
T_{gun}	2	10	Gun replacement time (years)	(Wenzel, 1991)‡
C_R	0	45	% of hunters in Canadian Ranger program	(DFO unpublished data)
bu	1	10	Bullets per hunter (per trip)	‡
c_{bu}	2	3	Cost per bullet (\$)	†
L	20	100	Gas per trip (Liters)	†
c_{gs}	0.9	1.1	Cost of gas per trip (\$)	†

† indicates value was obtained by in 2008 from Repulse Bay

‡ indicates value was estimated by authors with assistance of northern field researchers (Jack Orr and Blair Dunn)

¹ Other studies (Reeves, 1992b; Northern Economics Inc, 2006; Foote and Wenzel, 2009; Wenzel, 2009b) were considered along with collected values

Composition of body weight for narwhal has been noted as 30-35% of body weight as blubber, 25% muscle, and 10% skin (Reeves and Tracey, 1980). A summary of edible weights from the 1960s to the early 1980s (Ashley, 2002) indicate upper limits of 45% of body weight for beluga as muktaaq with some muscle, and 37% upper limit for narwhal muktaaq and some muscle. Reeves (1992b) listed multiple sources and values of utilization ranging from 6.9-45.7% of body weight for narwhals and 14-76% for belugas, although it was noted these ranges were higher than observed values within the same paper. Using the average weight for a narwhal (Heide-Jorgensen, 2002), with the amount of muktaaq taken from harvested whales (Wenzel, 1991, 2009b) yields values of 5.9% and 7.8% of the body weight utilized as muktaaq.

For belugas a trade between Nunavut and Nunavik of 2,268 kg of muktaaq from roughly 20-30 whales as noted by Tyrrell (2007) would yield 10.5-15.6% of body weight for an average sized beluga of 725kg (DFO, 2002a; NAMMCO, 2005a). More recent research on belugas estimate lower ranges from 8-10% of body weight consumed (Hrynyshyn, 2004). Estimates from field researchers were much lower at 5-12% of body weight being consumed as muktaaq or muscle (Jack Orr pers. comm., 2010). Taking into account the possible exaggeration for the upper ranges on the edible weights for both narwhal and belugas from early studies, the edible portion for belugas e_B and narwhals e_N were both set to the range of 5-25% of the body weight to include muktaaq and some muscle.

The cost of meat replacement per kg of meat for narwhal and beluga, c_{pN} and c_{pB} , was set to the next best alternative protein source based on values of a variety of meat products (eg., chicken, steak, and ground beef). The replacement cost of meat has been calculated for other hunting activities in Canada and Alaska in the past. Replacement values for other harvested animals have ranged from \$8.8 per kg for moose in Alaska for 2005 (Northern Economics Inc, 2006), \$8.50-\$10.00 per kg replacement of polar bear meat from the 1980s and 2002 (Foote and Wenzel, 2009; Wenzel, 2009b). The lower estimates of replacement value for polar bears were for communities using the meat as dog food, therefore this reflects the cost of dog food. In

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1990 narwhal and beluga muktaaq sold through the country-food store in Iqaluit for \$17.60-18.99 per kg and \$15.40 per kg respectively as they were imported from other communities, although prices are expected to have increased since then (Reeves, 1992b). Our replacement values are higher, based on a variety of chicken, beef, pork and seafood both fresh and canned. While beluga and narwhal meat may be used as dog food, our replacement values consider meat substitutes regardless of their use for human or dog consumption. Both replacement costs of narwhal and beluga, c_{pN} and c_{pB} , were set to the range of \$6.90-\$39.00 per kg, based on the cost of various protein sources collected from the local Co-op in Repulse Bay in 2008.

For beluga carvings, the number of teeth per beluga, T_B , used for carving was set from 0-2 per whale, as younger belugas caught have smaller teeth not generally used for carvings, and older whales can have prominent wear patterns in their teeth. Older teeth are generally unsuitable for carvings, meaning teeth are only extracted from certain whales. In general only larger vertebrae are used for carvings. Teeth and vertebrae are either collected as they are found from previous hunts or are left in the sun to bleach for years before being used as a carving (Jack Orr pers. comm., 2010). The amount of vertebrae per beluga, V_B , used for carving was set between 0 and 2, as many hunters do not collect the vertebrae, and not all vertebrae are suitable for carving. Narwhal incisor teeth are used for carving along with narwhal vertebrae. In male narwhals the upper left incisor erupts into a tusk which can be sold whole or used for carving. Female narwhals have 2 incisor teeth, F_{to} , thus 2 teeth available for carvings, with the model range set between 0-2. Males have 1 incisor tooth (after the tusk erupts), therefore M_{to} was set to a range of 0-1. Vertebrae taken from narwhal, V_N , was also believed to be low, and was set from 0-2 vertebrae per whale, based on the same reasoning as belugas. The distribution of vertebrae and teeth remained uniform, although only discrete values were used for sampling (values of 0, 1, or 2 only). Teeth and vertebrae are used on their own to make small carvings, or as part of a more elaborate carving which can include parts from various mediums from a variety of animals. The price of one carved tooth for beluga or narwhal, P_t , can range from \$20-\$60 as part of an earring set or

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up to \$200 if it contributes to a more elaborate carving. Price of vertebrae carvings, P_v , were set to the range of \$60-250, depending on the quality and size of the carving.

For males additional revenue is generated from tusks, and is dependent on the length of the tusk. Measurements of narwhals harvested in Pond Inlet from 1982-1983 show a tusk range from 136 to 236 cm (4.46 to 7.74 feet) (Weaver and Walker, 1988). Maximum lengths up to 202 cm have been reported in Greenland (Garde et al., 2007), with rare cases of tusks reported longer than 243 cm (8 feet) (Reeves, 1992a). The range for tusk length, L_{tu} , was set from 2.5 to 8 feet in the model. Tusks are either sold whole or used for carvings. Recent reports estimate the ratio of whole tusk sales to tusk carvings is high, based on exporting records (CITES, 2004), suggesting relatively few tusks are used for carvings. Therefore T_w , the percentage of tusks sold whole was set from 95-100%, with the remaining 0-5% used as carvings. The price for a whole tusks is the amount a hunter would receive if the tusk is sold to the local Co-op store. In 2008, Repulse Bay hunters were paid \$100 per foot for tusks up to 6 feet, and then \$15 per inch for every additional inch, this was used for prices of whole tusks, R_{wt} , in our model. Tusks that are turned into carvings are estimated to generate prices, P_{ct} , ranging from \$60-200 per foot depending on the size and quality of the carving.

Costs for each hunt are dependent on the number of hunters participating in each hunt. Based on 2006 census data (Statistics Canada, 2006), there were 2,310 aboriginal men over the age of 15 in the beluga hunting communities, and 1,150 aboriginal men over the age of 15 in narwhal hunting communities. Of these men it was assumed 10-40% of the ones in beluga hunting communities hunt belugas, M_B , and 20-50% of these men in narwhal hunting communities hunt narwhals, M_N . Women are generally not part of the hunt, although they do help with processing and are considered an important component of the overall activity, the number of men in each community was used as an indicator of the number of hunters. This is not to imply women do not participate or are unimportant to hunting in general, but rather the number of men was used to provide an estimate

as to the number of people participating in each hunt. In Repulse Bay, the hunting season for narwhal is shorter than for belugas in other communities. In 2007 specifically, the narwhal quota was reached before the end of the season, making it a successful hunt, with a large community involvement (Greer, 2007). Because of the short hunt season and high demand for narwhal, there is a higher proportion of participants for narwhal hunting set in the model, M_N . The estimated number of trips taken by each hunter per year was set to 10-15 for belugas, I_B , and 5-10 for narwhals, I_N , as the hunting season for narwhals is shorter, as the quota tends to be reached quite quickly in the hunting season. Group sizes of hunting trips were observed to be between 2-4 for the 2007 narwhal hunt in Repulse Bay (Greer, 2007), however for the model the range was extended to 1-5 hunters for both hunts, B_{gr} and N_{gr} .

Gear costs were set to the same ranges for both hunts. There are a range of guns used according to the hunting records from narwhal, with the most common caliber guns in order of frequency of use for hunting; .303, .338, .375, 6.5mm, .308, and the least common 458 (DFO unpublished data). The same gun types and proportions were assumed for beluga hunting. The cost of each gun, c_{gu} , ranges from roughly \$700-\$1200 as based on prices for .338 and .308 caliber rifles from Cabelas Canada, where a number of hunters purchase their guns (www.cabelas.ca). The .303 caliber rifles used for hunting are provided by the Canadian Ranger program. Community members, including hunters, can enroll in the Canadian Ranger program to assist the Canadian Forces in protecting their communities if necessary, and in return they receive a .303 caliber rifle and 200 rounds of ammunition each year in addition to clothing. Therefore, the cost of these rifles, 55% of the guns used to hunt narwhal in 2007 (DFO unpublished data), are not fully incurred by the hunters themselves, rather the guns are earned by participating in the Canadian Ranger program. The cost of all guns in the model, (C_R), was set from 0-45% of the total value to account for the proportion of hunters belonging to the Canadian Ranger program, and thus receiving .303 rifles from the program. Wenzel (1991) noted 4.3 years as a replacement time for guns used in polar bear hunts, with boats and boat motors lasting longer with

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replacement times of 6.9 and 4.7 years respectively. We assumed a range of replacement times for guns, T_{gun} , from 2-10 years within the model. For boats used in the hunts the cost, c_{bo} , was set from \$3,000-\$20,000 (J.Orr pers. comm 2010) with a replacement time, T_{bo} , from 4-10 years.

Community population size was taken from the 2006 Canadian census (Statistics Canada, 2006). For all beluga hunting communities there were 7,364 people, B_{pop} , and for narwhal hunting communities, there were 3459 people, N_{Pop} .

Table 6.2: Community statistics as provided by Statistics Canada Statistics Canada (2006) for Hudson Bay hunting communities

Community	Median Income (\$)	# people employed	# people in labor Force	# men 15 and over
Arviat	15,200	535	615	600
Chesterfield Inlet	21,184	140	160	105
Coral Harbour	14,029	250	310	215
Rankin Inlet	26,389	1010	1125	805
Repulse Bay	10,912	180	275	250
Sanikiluaq	14,368	205	250	240
Whale Cove	16,352	90	100	95

6.4 Results

Beluga

The total revenue from the beluga hunt ranged from \$57,667 to \$1,995,473 with a mean value of \$601,154. Of the total revenue, carvings from teeth and bones contributed an average of \$50,156, and meat contributed an average of \$550,997 identifying meat as a major contributor to beluga value. The total cost of this hunt ranged from \$52,090 to \$3,763,073 with a mean value of \$593,949, with boats having the highest cost per trip, followed by fuel, guns, and then bullets (figure 6.2). Economic value for beluga ranged from -\$3,709,037 to \$1,915,904, with the mean value of -\$9,399. The per capita economic value ranged from -\$503 to \$220 with a mean value of -\$1.

The opportunity cost of beluga hunting ranged from \$217,973 to \$718,212, with a mean value of \$445,514. When incorporating the opportunity cost into the total cost estimate, the mean total economic value decreases to -\$454,859 with the range -\$4,210,558 to \$1,407,560. Inclusion of opportunity cost decreases the per capita value of beluga hunting to -\$61.

When cost sharing from other hunting activities is incorporated into the model without opportunity cost, the mean economic value of the hunt increases from \$266,504 for cost sharing with one other hunting activity (2 hunting activities altogether), to \$487,184 for cost sharing with 9 other hunting activities. The mean per capita economic value increased from \$36 to \$69 when costs were shared with 1 to 9 other hunting activities (figure 6.3). However, inclusion of opportunity cost causes a decrease to the per capita economic value which now ranges from -\$24 to \$5 for cost sharing with 1 and 9 other hunting activities respectively.

Narwhal

The total revenue for the narwhal hunt ranged from \$81,267 to \$1,413,947, with a mean value of \$529,928. Average revenue from meat was \$366,100, with tooth and vertebrae carvings from female narwhal generating an average of \$9,339, and tusks, teeth, and vertebrae from the male narwhals valued

6.4. Results

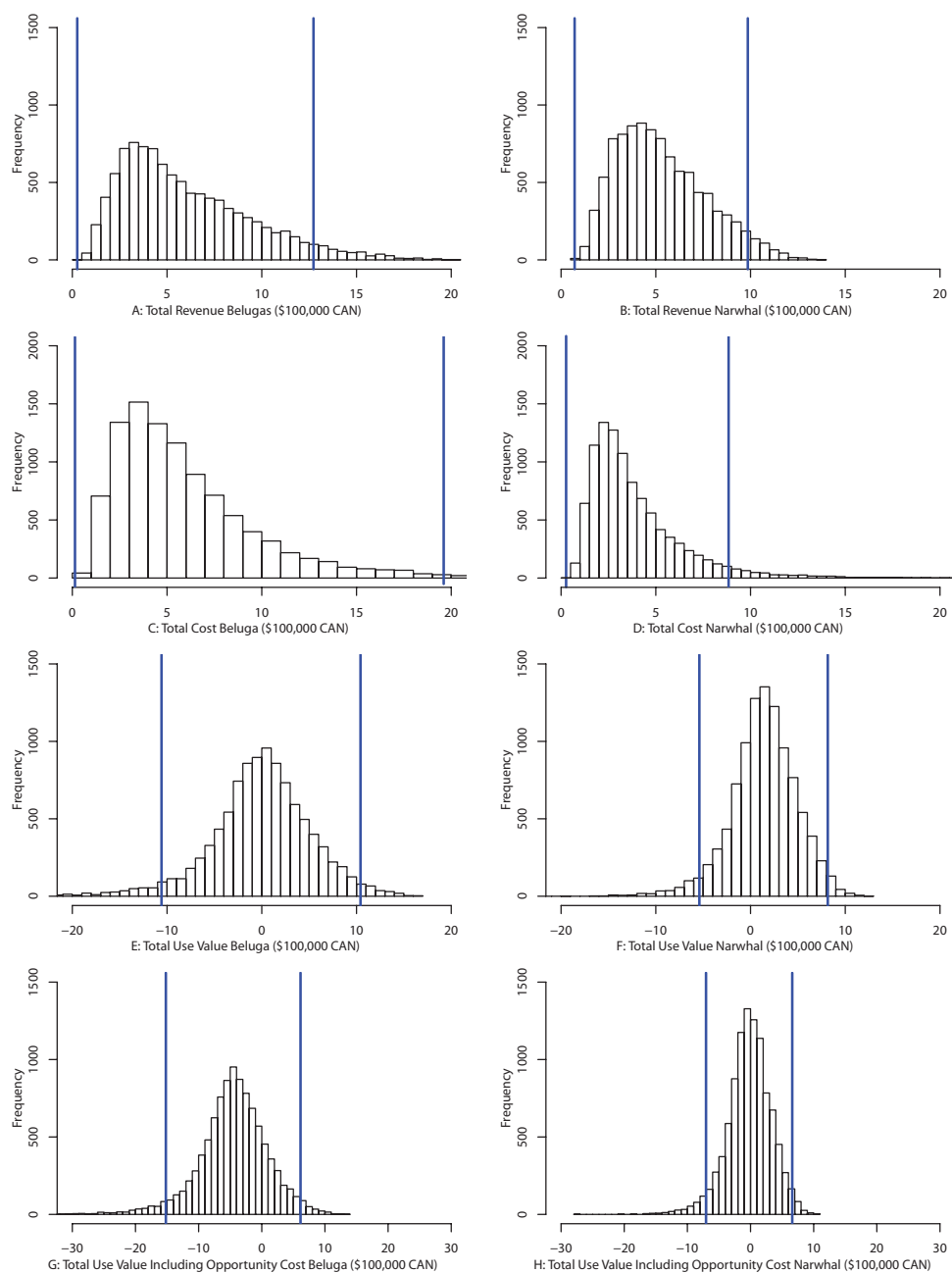


Figure 6.2: Distributions and 95% CI for Total Revenue (TR), Total Cost (TC), Total Use Value, and Total Use Value including Opportunity Cost. All values are presented in Canadian Dollars

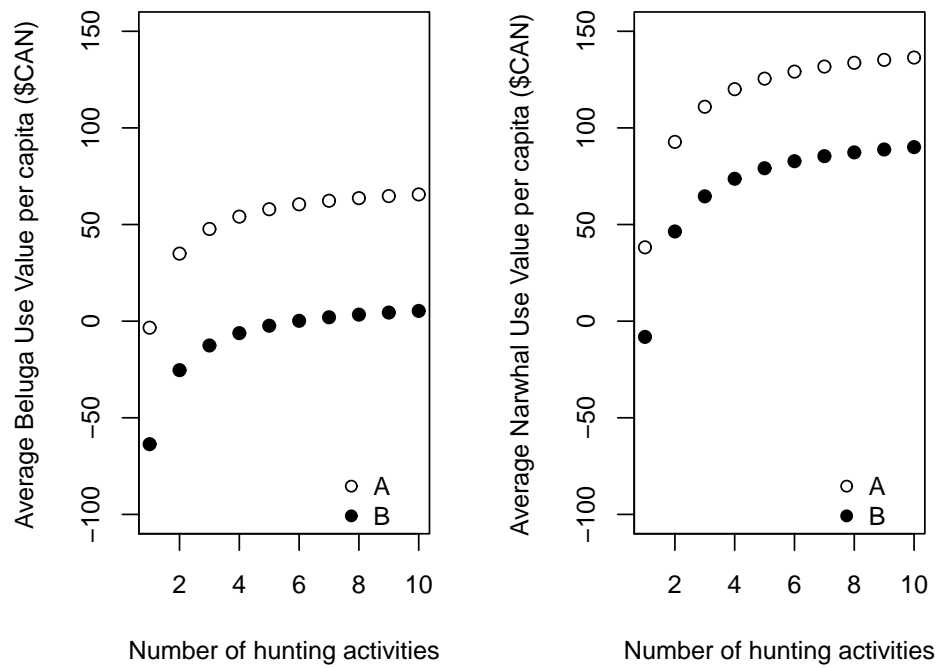


Figure 6.3: Average per capita use value for beluga and narwhal hunts under (A) cost sharing with other hunting activities, and (B) cost sharing with economic values calculated to include opportunity cost. 2 hunting activities implies either the beluga or narwhal hunt plus one additional hunting activity

at \$154,487 on average. The total cost ranged from \$58,273 to \$2,279,463 with a mean value of \$376,821. As in the case of belugas, boats had the highest average cost, followed by fuel, guns, and then bullets. This resulted in the economic value ranging from -\$2,120,367 to \$1,193,315 with an average value of \$133,278. The per capita economic value ranged from -\$602 to \$348, with a mean value of \$44 (figure 6.2).

The opportunity cost of narwhal hunting ranged from \$69,763 to \$288,113 with a mean value of \$160,013. Economic value decreased to a mean value of -\$26,735 with a range of -\$2,301,919 to \$1,025,006 when including opportunity cost, and the per capita values lowered to a mean value of -\$7.

The economic value and the per capita economic value show increases when costs are shared with other hunting activities. The economic value increases from a mean of \$133,278 to \$331,500 when costs are shared between 2 hunting activities (narwhal hunting plus one more) up to \$472,077 for cost sharing with up to 9 other hunting activities. This leads to an increase in per capita economic value from \$44 per person to \$96 for 2 hunting activities, and continues increasing to \$137 when costs are shared among 10 hunting activities (figure 6.3). However, with opportunity cost considered, these per capita values decrease to \$46 and \$90 for cost sharing with 1 and 9 other hunting activities respectively.

Opportunity Cost and Cost Sharing

Table 6.3 identifies the average economic value when costs are shared with other hunting activities, while figure 6.3 shows the mean per capita values. Although narwhal has a higher value when calculating hunting activities, cost sharing results in beluga hunting having a higher value.

Value Per Community

While all calculations made are based on all communities investing the same costs, and receiving the same revenues, in reality this is not the case. Based on the total revenue and the number of whales landed, the value from each hunt per community was estimated based on a mean revenue of \$3,163 per

6.4. Results

Table 6.3: Cost sharing results: mean values presented for total economic value of beluga and narwhal PI_B and PI_N respectively. Economic value is recalculated including the opportunity cost of each hunt.

# Hunting Activities	Π_B	Π_B including opportunity cost	Π_N	Π_N including opportunity cost
1	-9,399	-454,859	133,278	-26,735
2	266,504	-179,009	321,500	161,486
3	358,454	-87,059	384,240	224,227
4	404,429	-41,084	415,611	255,597
5	432,014	-13,499	434,433	274,419
6	450,404	4,890	446,981	286,967
7	463,540	18,025	455,944	295,930
8	473,392	27,877	462,666	302,653
9	481,054	35,540	467,895	307,881
10	487,184	41,670	472,077	312,064

beluga and \$6,542 per narwhal (table 6.4). Ignoring costs for a moment, results indicated that Repulse Bay generated the highest revenue with nearly half a million dollars being contributed by narwhal. Not only does this community benefit from a majority of narwhal catches in Hudson Bay, but the added value of hunting belugas identified a disproportionate amount of revenue being generated in this community compared to other communities.

Table 6.4: Contribution of revenue to each community

Community	# Landed	Belugas	Beluga enue (\$)	Rev-	Opportunity Cost Beluga Hunting (\$)	# Landed	Narwhal	Narwhal enue (\$)	Rev-	Opportunity Cost Narwhal Hunting (\$)
Arviat	50		158,150		67,855	—		—		—
Chesterfield In- let	12		37,956		16,674	—		—		—
Coral Harbour	7		22,141		20,924	—		—		—
Rankin Inlet	38		120,194		163,282	9		58,878		136,960
Repulse Bay	21		66,423		15,326	72		471,024		12,803
Sanikiluaq	52		164,476		24,204	—		—		—
Whale Cove	10		31,630		11,917	0		0		10,119

6.5 Discussion

In 2007, the total revenue from beluga hunts was higher than that of narwhals, but overall, the narwhal hunt has a higher net economic value. The main reason for this difference is due to the costs of hunting belugas being higher. As the costs of guns, boats, bullets, and gas were constant between the two hunts, the discrepancy in total costs stems from the number of hunters and the number of trips taken for each of the hunts. Narwhal hunting is more focused compared to belugas, as individual hunters are eager to be part of the community quota before it is filled. When considering the revenue generated per whale, narwhals are more valuable at \$6,542 per whale on average compared to belugas at \$3,163. While some of this can be attributed to tusks from male narwhals, the weight of the whale is also important, considering the weight for narwhals used in the model was higher than for belugas. In the case of narwhals, the value of meat (muktaaq and muscle) is higher than that of carvings and tusks. While male narwhals have a higher use value (higher body weight and additional revenue from tusks), the value of meat from narwhals contributes roughly 70% of the total use value of narwhals in this model.

For these communities, between 50-60% of people over 15 earn an income, with median incomes ranging from \$10,912 in Repulse Bay to \$26,389 in Rankin Inlet (Statistics Canada, 2006). Using Repulse Bay as an example, the economic use value (not including cost sharing or opportunity cost) per whale equates to \$38 per beluga and \$1890 per narwhal. Repulse Bay thus generates \$136,878 from hunting whales, as the distribution of catches is not even across communities (table 6.4). Repulse Bay has the lowest median income of all communities at \$10,912 with 375 wage-earners, yet the highest value from whaling. The value from whales is the equivalent of 3.3% of the income of each wage earner, meaning each wage earner would have to increase his/her annual income to make up for this loss in the event whaling ceased. The value for other communities would be lower due to a combination of lower contributions of value from whales, as the catches are lower, in addition to higher annual incomes.

The per capita use values of \$44 and -\$1 for narwhal and beluga are lowered when considering time spent hunting (opportunity cost) to -\$7 and -\$61 per person. Model costs of obtaining and operating gear are high enough to negate the value of meat and crafts derived from the whales. Considering the polar bear hunt in Clyde River, gear costs range from 44-80% of a hunter's income, with these costs limiting one's ability to participate in hunting activities (Wenzel, 2009b). Hunters who are employed (wage-earners) are better able to afford and maintain hunting equipment (Wenzel, 1991). Hunting analyses of other species have also identified low economic use values. Economic analysis of seal hunting in Clyde River in the 1980s identified revenues of \$1133 per hunter (not per capita), but once costs were considered hunting operated on a deficit (Wenzel, 1991). The subsistence economic value of moose (meat only) was calculated to be \$633 per hunter in 2005 (Northern Economics Inc, 2006), again this would be lower if calculated on a per capita basis. One analysis of multiple subsistence hunting activities in Alaska identified an economic value close to zero once opportunity costs were included Colt (2001). The per capita economic values for the narwhal and beluga hunts identify that although revenues may be substantial, considering investments of gear and time, participating in hunting activities is a timely and costly endeavour.

There are perceptions that hunting activities in the Canadian north are based on financial desire (Wenzel, 1991), although the model results presented here, and past economic studies indicate there may be other motivations. It has been noted that money is necessary to facilitate hunting activities, rather than being the end goal (Nuttall, 2005). Anthropological literature outlines the cultural importance of hunting activities as well as views on animals as a resource (see Wenzel, 1991; Freeman and Foote, 2009; Schmidt and Dowsley, 2010), although it is not quantified in this analysis. These hunts (and others) most likely have high cultural values driving hunters to participate in hunting activities with low financial returns. One important cultural aspect of the hunt is resource sharing. The concept of sharing food across individuals, families and communities is paramount to the cultural stability in northern communities (Nuttall, 2005). It has been

reported that this system of sharing is a socially, not economically-based norm (Nuttall, 2005).

Despite contributing only a small fraction of the total income to the community, hunting will almost certainly continue to occur due to the cultural and community values associated with these activities. The hunting and sharing (distribution) of country foods, in addition to other resources, is a culturally significant exercise in many northern communities (Nuttall, 2005). It is estimated that 96% of Inuit households share food with the community (Tait, 2001), in addition to the community participation necessary to land and process a whale, and the celebration of the hunt as a core cultural feature to these communities (Freeman, 2005). The value of participating in hunting activities (non-use value) to Inuit provides intangible benefits to hunters and provides a source of identity (Wenzel, 1991; Reeves, 1992b). So while the use value of these hunts is sizable when looking at the hunt as a whole, or on a community basis, the total value to the individual hunter (use and non-use value) is likely much higher than what our current data and model can possibly capture. In this regard, the total value of beluga and narwhal hunts to community members may be underestimated in our study.

There are likely other reasons why people would continue to hunt. First, costs could be lower in reality, as previously mentioned, through cost sharing with other hunting activities. Second, subsidies also lower hunting costs, as they are shown to do with fishing (Sumaila and Pauly, 2006; Sumaila et al., 2010). Third, opportunity costs are more likely to be overestimated within the model, rather than underestimated.

Continued building on the current model to include additional variables for both costs and revenues will further expand understanding of hunting activities. Future incorporation of additional variables will affect the model in many ways. Revenues from whales outside of food and arts/crafts values include the previously mentioned cultural values, added health benefits and values to scientific research. In the model, muktaaq was assigned a substitute through the next best available protein such as beef, pork, or chicken from the local store. However, in nutritional terms, these may not

be practical substitutes. Marine mammal blubber and skin contain high levels of retinol (a form of vitamin A), vitamin B, vitamin C, and polyunsaturated fats in addition to being high in protein, while marine mammal muscle is high in iron and zinc Geraci and Smith (1979); Kinlock et al. (1992); Hidirolou et al. (2008). Diets with higher contributions of country foods and polyunsaturated fats protect against cardiovascular disease with store bought foods having lower values of polyunsaturated fats (Kinlock et al., 1992). The differences in nutritional value between country foods and store bought foods should be considered a limitation of this modeling exercise. Scientific research also benefits from harvested animals. Samples of fat, muscle and other organs are collected by hunters and sent to researchers for analysis. From these samples diet information, health of the whales and genetic analysis can provide valuable data for stock management.

Estimates providing the costs associated with hunting will need to be expanded for more precise economic values of both hunts. Information beyond what is presented in the model may alter hunting costs up or down, ultimately affecting the economic value. Additional costs of equipment maintenance, inclusion of camping gear (stoves, tents, food for multi-day trips) and processing gear (knives, equipment for drying meat) will result in lower economic values than presented in this paper. However, other factors such as cost sharing would lower costs resulting in higher economic values than presented. Although values were presented as though all cost incurred (fixed and variable) were borne solely for the purpose of the individual hunts, this is not representative of hunting in the north. Repulse Bay, for example, participates in both the narwhal and beluga hunt. If hunting activities were combined using the same gear, and narwhal were only hunted opportunistically from 'beluga hunting trips' then in theory we might assume no costs associated with the narwhal hunt because in this case it would be considered a non-target species. Hunting activities in the north also target a variety of seals, caribou, polar bears, and birds, fish and shellfish. It is almost certain that there is some degree of cost sharing occurring already. Figure 6.3 illustrates the increase in economic value due to cost sharing. Both hunts show an asymptotic shape indicating the greatest increases are happening when

costs are shared between 2-4 activities, which is likely already occurring in reality.

The issue of subsidies has not been fully addressed in the model. We have incorporated the fact that discounts on guns and bullets are offered to some members of the community, as information from harvested narwhals indicates the majority of guns used for hunting (and bullets) were obtained from the Canadian Ranger program. Other subsidies are known to exist for hunters, however the magnitude of the value is not known, nor how these subsidies are filtered down to the hunters. Information regarding numerous programs available through Nunavut Tunngavik Inc. (NTI) aimed to assist Nunavut hunters is available online (<http://www.tunngavik.com/programs-and-benefits/frequently-asked-questions/hunters-harvesters/>). Various programs under NTI offer subsidies, such as the Nunavut Harvester Support Program (NHSP). The NHSP allows for discounts or assistance under various criteria. These programs offer hunting gear at a subsidized cost, or money to purchase gear through the local HTO, thereby lowering the costs associated with hunting. Furthermore, since carvings and tusks are generally sold through the local Co-op before they are further distributed at higher prices, the Co-op generates revenue from these sales. While the amount or revenue is unknown, profits generated from the Co-op are re-invested in community programs, thereby adding value to the community through these sales. It is also possible for individual hunters/carvers to sell their products directly to art dealers or travelers generating additional revenue directly.

The opportunity cost calculated within the model is possibly an over-estimate, however more research would be needed to improve estimates. Hunters may make trips after working hours or on the weekends, when not interfering with work, which would lower the opportunity cost. In addition, members of the community have been known to leave work when whales were known to be in nearby areas, forgoing work for hunting. This would imply hunting activities are more important than earning a wage, thus emphasizing the cultural value of the hunt.

While values in this model are derived from hunting, there is the possibility of generating revenue through other avenues such as whale watching.

It was estimated that for 2003 over 13 million people globally participated in whale watching, spending over \$1.6 billion USD (Cisneros-Montemayor et al., 2010). Yet the notion that whaling and whale watching cannot coexist must be taken into account. Highest potential revenue from whale watching activities exists in locations where tourism infrastructure already exists (Cisneros-Montemayor and Sumaila, 2010). While many northern communities lack a significant flow of tourists, potential exists for the opening of whale watching endeavors. More research is needed to identify the scope of these possibilities including the potential desire for northern communities to participate. Polar bear hunting activities combine sport based "trophy hunts" for non-natives along with traditional hunts (Dowsley, 2010) indicating some communities may be willing to participate in multiple activities to generate revenue.

Perhaps what is most informative regarding this model is the revenue generated from both hunts averages just over \$1.1 mil CAN for the 2007 year, with most of the revenue generated as edible products. While this is considered an underestimate for reasons previously mentioned, the total value pales in comparison to the total value of commercial fisheries within Canada, which was \$1.95 billion for 2007 (DFO, 2009b). In the case of the narwhal hunt, it is often implied that hunting activities are driven by potential profits from male narwhal tusks. However, for the communities specified in this model, only 56% of catches (from Repulse Bay) were males indicating they were not the sole targets of the hunt at least for the 2007 season. It would appear due to the relatively total value of these whale hunts, when compared with total Canadian fisheries values and the contribution to local annual income, motivations for hunting are generated from a cultural perspective.

If, in the event harvesting of whales is not possible in the future due to biological limitations, the economic ramifications to the communities not only in Hudson Bay, but other areas of Nunavut and Quebec, should be taken into account. The trade ban of narwhal products outside of Canada will have impacts to Hudson Bay communities, yet lost revenue appears negligible compared to costs associated with hunting. As the preliminary

6.5. *Discussion*

details of these hunts have been presented here, more research is needed to gain a better understanding of various aspects of these activities in northern communities.

Chapter 7

Conclusions

7.1 Chapter 1

Chapter 1 provides the background for the dissertation. This chapter focuses on the history of management and a brief ecological background to each area. Both areas demonstrate a history of resource use, changing throughout time. In addition, sensitivity to climate change highlights the desire to gain a better understanding of these ecosystems. Here the modelling framework is introduced for chapters 2-5. Chapter 6 is necessitated in order to determine the motivations behind harvest in Hudson Bay. Ideally this will aid in management strategies. Main conclusions are presented by geographic area rather than chapter progression in the thesis.

7.2 Hudson Bay

Chapter 2

Chapter 2 highlights the construction of the Ecopath model and simulations recreating past changes in the ecosystem. Perhaps the most important aspect of this research is not the model itself, but the model as a tool to identify gaps in existing data. Limited studies have occurred in the area, as there is not a lot of resource use (outside of subsistence harvest) in the area. The quality of a model is a reflection on the data used to create it, and while there are many studies incorporated into the Hudson Bay ecosystem model, some liberties were taken to fill in gaps in data. Despite this, the Ecopath with Ecosim model framework allows for the estimation of parameters through food web interactions, such as fish biomass. Total fish biomass

was estimated to be $3.42 \text{ t} \cdot \text{km}^{-2}$ for 1970, based on diet needs of predators, energy produced by lower trophic levels, and structure of the diet matrix.

Re-creation of the past ecosystem identifies changes in fish community composition can be explained through benthic-pelagic decoupling. Declines in the ice algae to benthic pathway caused by losses in sea ice, and increases in pelagic production to zooplankton favor planktivorous fish over benthic feeding fish. This is supported by alterations in bird diets, whereby planktivorous fish has been shown to increase throughout the time span of the model simulation (Gaston et al., 2003). Within the model, lower trophic levels are more heavily influenced by environmental drivers used. The effects become dampened to higher trophic levels. However, higher trophic levels are more heavily influenced by harvesting activities. Populations identified within the model to have shown declines related to harvest are; polar bears, narwhal, eastern Hudson Bay belugas and bearded seals.

In Hudson Bay there is a need for more research on all ecosystem components, however fish were identified to be the weakest link of the model. Basic surveys of fish in the region would be extremely useful for future research and model validation. As only 2 plankton studies have been conducted (Harvey et al., 1997, 2006) continuation of surveys over time will allow researchers to form a better picture of changes. For example surveys on the Hudson Bay narwhal population were completed in 1984 and 2011 (Richard, 1991, 2010) identifying declines in the population. Poor weather conditions for the 2011 survey may have resulted in an underestimate of the population (DFO, 2010a). With only two reference points for this population, additional research will be important for confirming trends. It is expected as more research is conducted, the model will need to be updated as appropriate.

Chapter 4

Continuation of environmental drivers into the future reveals the further deviation from a benthic to a pelagic dominated ecosystem. Biomass changes in lower trophic levels up to fish are a result of further shifts from ice algae

to pelagic production. Harvest is an important factor in determining the declines of marine mammal species. Species previously identified to show slight declines due to harvest, cannot continue to be harvested at current rates. Narwhal, eastern Hudson Bay beluga, polar bears, and walrus, will be removed from the ecosystem within the model if current harvest levels continue into the future, while harp seals, ringed seals, harbour seals, and beluga (western Hudson Bay and James Bay stocks) are more robust to hunting pressure.

Interestingly, with the changes in species composition the trophic level of the ecosystem remains constant from the 1970s to 2069. Even with large reductions in top predators, the ecosystem remains stable and model results show slight increases in biomass in the future. The increase in total biomass is a result of continued increases in zooplankton piscivorous fish. The larger, more stable marine mammal stocks increasing over time compensate for reductions in others and prevents declines in ecosystem trophic levels.

While future simulations present an interesting insight as to potential future states of Hudson Bay, research into future impacts of climate change would be futile without a better understanding of the current ecosystem. Rather than recommend research activities directed into the future, energy would be better spent gaining a firmer grasp on the current ecosystem. However, that being said, the past and future models identify the vulnerability of certain marine mammal stocks to current and future over-harvest. It would be wise for managers to focus on the current harvest levels of these stocks to ensure their continued survival.

Chapter 6

Simulation results from chapter 6 estimates the total economic use values be a negative value of \$9399 for the beluga hunt and a positive value of \$133,278 for the narwhal hunt in 2007 for Nunavut Hudson bay communities. As costs were calculated for each hunt independently, cost sharing analysis revealed that if hunting costs were shared with one other hunting activity the total use value would increase to \$266,504 for beluga and \$321,500 for narwhal

hunts. Narwhals provide a higher use value per whale than do belugas due to the added value of their tusks. Despite this, the total revenue was higher for the beluga hunt as more belugas are harvested than narwhals. More communities harvested belugas in this study leading to greater costs across communities. When these values are broken down on a per capita basis, the economic use value for beluga was negative \$1 and for narwhal was \$44.

One possibility for low values is due to errors in parameter estimation. While this is one of a limited number of economic assessments on hunting activities in the Canadian Arctic, parameter estimates were not easy to come by. Future research into obtaining more precise parameter estimates in addition to expanding the model will be useful in developing the overall understanding of hunting activities. One area lacking understanding, highlighted throughout this research, was the use of subsidies for hunting gear. As Nunavut is newly established, this may be one of the main reasons for lack of transparency or literature on the topic of subsidies. Contacts working for the Canadian government struggled to identify how subsidies are regulated in the north. This would be an important addition to the model, and research in this area would benefit many other areas of research.

The most interesting results from this chapter is the low values indicate that harvest may be driven by non-economic factors such as cultural importance. Many studies, mainly anthropological, have highlighted the importance of hunting for cultural identity for northerners (Freeman et al., 1998; Freeman, 2005). The economic analysis provided supports this theory. Due to the low per capita economic use value, it is highly possible non use values provide motivations for hunting.

Recommendations to Management for Hudson Bay

Managers will have to face decisions on how to navigate within their limits, not only the Nunavut and soon to be established Nunavik governments, but within the realm of their capabilities and managers. Of the two main threats studied (climate change and hunting), only harvest can be controlled

by management. Climate does impact the ecosystem, but that is out of the realm of control for managers. The focus is on harvest and if altering the current harvest levels for HB is in alignment with management objectives. Ecologically, it would prevent the declines of narwhal, eastern Hudson Bay beluga, polar bears, and walrus. However, there are many communities who rely on subsistence harvest of these and other species for food and cultural identity.

Sustainable harvest is ideal for fisheries in order to perpetuate the resource so it can continue to be harvested, thus increasing the value over longer time frames. If motivations for hunting are derived from cultural values as suggested by chapter 6, management will need to take this into consideration. Preservation of resources for future generations may come at a cost to current hunting activities. Both the Nunavut and Nunavik land claims agreements state principles of conservation to maintain the natural balance of ecological systems while providing continued access to hunting (Nunavut Land Claims Agreement, 1993; Anonymous, 2006). Species shown to decline in the past or future model simulations due to hunting will require reductions in catches if the populations are to be sustained long term. Both land claims agreements also indicate it is ultimately the governments' responsibility to manage wildlife. Decisions by the federal government (DFO) to restrict hunting have yet to occur in Hudson Bay, however action may be required in the future.

7.3 Antarctic Peninsula

Chapter 3

Chapter 3 describes the Ecopath model for the Antarctic Peninsula and Ecosim simulations recreating past changes in the ecosystem. The first main finding was the overestimation of krill in the diets of predators. It is possible that due to the high variability of diet studies (Hyslop, 1980), the contributions of krill to higher trophic levels may be lower than the literature indicates. Recreation of past trends identified sea surface temper-

ature as a suitable driver for warmer water species. This gave a lower sum of squares values than did simulations for the Southern Oscillation Index, air temperature, or open water extent, resulting in a better fit for the salp group. Simulations of past changes show an overall decline in primary production as ice algae declines. This results in lower krill biomass and lower biomasses of predators.

Under a constant climate scenario in the model, higher levels of marine mammals could be supported indicating they may not be at carrying capacity. This would imply that since marine mammals stock had decreased due to large harvest pressure, under a scenario where there are more resources (krill) available, the ecosystem could withstand more mammals. However, under the past conditions recreated, marine mammal species decline due to the environmental impacts on krill. Increasing past catches to current quota levels throughout the simulation shows slight differences from the past recreated scenario ($\pm 3\%$ of biomass) indicating environmental factors have higher impacts on the ecosystem.

Chapter 5

Future simulation continued in chapter 5 identified further reductions in sea ice, ice algae, krill, and krill predators. Declines in the ecosystem continued from the past model, with mean trophic level remaining stable indicating declines in biomass were even across all trophic levels. Environmental drivers were primarily responsible for the declines of krill when considering current harvest levels. When catches were increased to quota levels, further reductions in krill ensued. Harvest scenarios where future catches are at current quota levels and 25% of the catch is taken from the juvenile krill group cause an instability within the model. Length frequency distributions of krill catches (Jackowski, 2002) show immature krill are taken, and appear to be less than 25%, but the exact contribution to the total catch is unknown.

Copepods in the model have the ability to increase at varying degrees in future scenarios. The scenarios, harvest scenario H2b in particular, highlight

the potential for copepods to replace krill and other prey items for some predators (myctophids, small deep demersals, *P. antarcticum* and some marine mammals). Omnivorous organisms such as krill demonstrate potential dietary reduction in primary producers and increases in copepods, thus increasing their trophic level. This would then increase the trophic level of krill predators, as an overall lengthening of the food chain.

Increased winter based studies may highlight seasonal shifts in predator diets away from krill, as the model suggests. Numerous studies have been completed assessing the impacts of different environmental variables on krill survival (Atkinson et al., 2004; Ross et al., 2008; Lee et al., 2010; Flores et al., 2011), and will likely continue due to the importance of krill in the food web. Selected future model scenarios suggest copepods as a replacement for krill, future studies should include or focus on copepods or other zooplankton groups to identify their importance in the food web. Stable isotope analysis, particularly changes over time, would provide a useful comparison to model results, specifically for krill.

Recommendations to Management for the Antarctic Peninsula

Currently, CCAMLR utilizes a krill yield model to determine harvest levels and to prevent irreversible damage to the ecosystem due to over-harvest (CCAMLR, 1980). However, the current model is a single species approach which incorporates predator demands and environmental variability. Management should consider expanding their current krill yield model to incorporate harvest on juveniles, and perhaps build into reporting strategies a way to determine the sexual maturity of krill so the contribution of juveniles can be estimated. Indirect effects of krill harvesting have been difficult to incorporate into models in the past (Constable et al., 2000). Past and future simulations in the thesis can be used to tease out some of the indirect effects as to provide this information to managers. Additional, more focused simulations could be constructed for specific management issues if needed now that the model structure exists.

CCAMLR management strategy encompasses an ecosystem approach and strives to ensure there are enough resources to meet ecosystem demands when considering quotas for krill and other species (CCAMLR, 1980). However it appears as changes in climate progress, the impacts to krill will become more prominent leaving less to be harvested without affecting predators. While harvest is not the primary cause of krill declines, it does further reduce a strained resource. Managers will be forced to choose whether to protect as much as the resource as possible to help thwart the effects of climate change, or continue harvesting.

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Appendix A

Hudson Bay Ecosystem Model Parameters and Details

A.1 Model Parameters by Functional Group

Marine Mammals

All marine mammals which inhabit the model area were included in the model. In addition, many species have been shown to be representatives from genetically distinct stocks, and therefore have been split into individual functional groups. For example, there are three stocks of polar bears within the model area, each with differing population trends and hunting quotas, and were therefore considered different stocks and functional groups within the model. Four species of cetaceans (bowhead whales, narwhals, belugas, and killer whales) are seasonal residents in Hudson Bay. For these functional groups their impact on the ecosystem is relative to the amount of time spent in the area and the proportion of annual feeding occurring during their time in Hudson Bay. A weighted biomass was designated to each of these groups to represent their respective impact on the ecosystem, so that if a group of whales resided in Hudson Bay half of the year and half of their feeding occurred during this time, then their weighted biomass would be half of the total population biomass (50%) to account for this. Individual estimates are given within functional group parameters. For all marine mammal groups the following equations were used to calculate input parameters (parameters for all marine mammals are in table A.1).

A.1. Model Parameters by Functional Group

Biomass was calculated by multiplying the number of individuals by average weight of individuals (in tonnes), then divided by the model area (km^2). Mortality rates (P/B ratios) were calculated for each species using the life table based on natural mortality (Barlow and Boveng, 1991)., and compared to published values where available (full equations for P/B calculations are available in appendix B). Mortality from hunting was calculated as the biomass harvested/total biomass, and was added to the natural mortality to give the final P/B ratio. Q/B: Consumption (Q/B) was calculated using equation A.1 (Hunt et al., 2000; Guenette, 2005);

$$E = aM^{0.75} \tag{A.1}$$

where E is the energy required per day (Kcal/day), M is the mean body weight (in Kg) and a is a coefficient representing each group of marine mammals (a=320 for otariids, 200 for phocids, 192 for mysticetes, 317 for odontocetes, and 320 for sea otters). Energy contents of food items was provided by various authors as summarized in Cauffman and Heymans (2005).

Table A.1: Input parameters for marine mammal functional groups. Mean weight is provided in Kg and Longevity is provided in years. Calculated (calc.) values and values used in the model are presented in the case they differ. Mortality (M) is presented as an annual value (y^{-1}) for both the calculated natural mortality and hunting mortality. Consumption/Biomass (Q/B) and Production/Biomass (P/B) are also presented as annual values (y^{-1}).

Species	Pop Size	Source	Mean Weight	Source	Longevity	Source	M (calc.)	Hunt M	Model P/B	Calc. Q/B	Model Q/B
Polar Bear WHB	1200	Lunn et al. (2002)	300	Stirling and Parkinson (2006)	25	Stirling (2002)	0.096	0.033	0.129	3.029	2.08
Polar Bear SHB	1000	Lunn et al. (2002)	300	Stirling and Parkinson (2006)	25	Stirling (2002)	0.096	0.058	0.154	3.109	2.08
Polar Bear Foxe	3000	Aars et al. (2005)	300	Stirling and Parkinson (2006)	25	Stirling (2002)	0.096	0.024	0.12	2.849	2.08
Killer Whale ¹	20	Higdon and Ferguson (2009)	4689	Ford (2002)	80	Ford (2002)	0.048	0.051	0.151	4.998	4.998
Narwhal ¹	2710	Richard (1991)	1300	Heide-Jorgensen (2002)	115	Garde et al. (2007)	0.083	0.008	0.084	18.696	26.182
Bowhead ¹	64	Higdon 2009 (unpublished data)	31076	Trites and Pauley (1998)	200	George et al. (1999)	0.018	0.003	0.021	5.475	5.475
Walrus N	2500	Mansfield and St Aubin (1991)	1037.5	Kastelein (2002)	35	Kastelein (2002)	0.141	0.031	0.172	41.238	47.123
Walrus S	500	Richard and Campbell (1988); COSEWIC (2006)	1037.5	Kastelein (2002)	35	Kastelein (2002)	0.088	0.009	0.097	29.56	33.778
Bearded Seal	15000	Lunn et al. (1997)	275	Kovacs (2002)	25	Kovacs (2002)	0.131	0.045	0.176	13.848	14.262
Harbour Seal	1000	assumed	76	Burns (2002)	29.5	Trites and Pauley (1998)	0.123	0.002	0.125	18.612	18.612
Ringed Seal	600000	Smith (1975)	42.5	Trites and Pauley (1998)	43	Miyazaki (2002)	0.15	0.008	0.158	16.05	17.272
Harp seal	8000	Assumed (Ferguson pers. comm)	130	Lavigne (2002)	30	Lavigne (2002)	0.112	0.014	0.126	15.66	15.66
Belgua E ¹	4200	Hammill (2001); Gosselin (2005); Hammill et al. (2009)	725	DFO (2002a); NAMMCO (2005a)	50	Harwood et al. (2002); Stewart et al. (2006)	0.044	0.032	0.066 ²	21.448	21.448
Belgua W ¹	50,000	COSEWIC (2004b); NAMMCO (2005a)	725	DFO (2002a); NAMMCO (2005a)	50	Harwood et al. (2002); Stewart et al. (2006)	0.0587	0.005	0.064	16.713	16.713
Beluga James ¹	1842	Gosselin et al. (2002)	725	DFO (2002a); NAMMCO (2005a)	50	Harwood et al. (2002); Stewart et al. (2006)	0.057	0.019	0.087 ²	16.623	16.623

¹ indicates biomasses were adjusted to 50% to account for roughly 50% of their time spent in the model area.

² indicates P/B for Eastern Belugas and James Belugas also account for migrations which were added in the fitting process

Polar Bears (*Ursus maritimus*)

Three of the nineteen polar bear populations (Paetkau et al., 1999) overlap with the Hudson Bay ecosystem model area; the Western Hudson Bay population, the Southern Hudson Bay population, and part of the Foxe Basin population (see Stirling et al., 1999, for polar bear stock delineations). These three populations were included in the model under different functional groups corresponding to each population (Western Hudson Bay, Southern Hudson Bay, and Foxe Basin). Being at the southern range of their limits in HB, climate change is believed to be an important factor in determining the health of these populations. Since polar bears rely on ice for foraging, extension to the ice free summer caused by melting is believed to increase nutritional stress. In addition, because these southerly populations already experience longer summers than their northern counterparts, they are thought to be more vulnerable to declines in sea ice (Stirling and Derocher, 1993; Stirling et al., 1999). The Foxe Basin (FB) and Western Hudson Bay (WHB) populations are believed to be declining, while there have not been enough surveys to determine trends in the Southern Hudson Bay (SHB) stock (Aars et al., 2005). In addition each population is subjected to different hunting pressures depending on the communities within their respective ranges.

While diets vary among populations, ringed seals are the most important food item in all polar bear populations, followed by bearded and harp seals (Peacock et al., 2010). Polar bears have also been known to take walrus, beluga, narwhal, seabirds, and waterfowl (Stirling, 2002). Scat analysis of western and southern HB polar bears from the late 1960s indicated foraging on birds (primarily from the family Anatidae- ducks, swans, and geese), mussels, urchins, other unidentifiable invertebrates, and berries in the late summer and autumn (Russell, 1975; Derocher et al., 1993). Although it is likely that these prey items are also consumed by the Foxe Basin population, it is believed the WHB and SHB may consume a greater portion of birds, invertebrates, and plants in their diets.

Polar bears were traditionally hunted for food and clothing, a tradition

which still exists today. Quotas have been imposed on each of the stocks by corresponding jurisdictions in Nunavut, Ontario, Manitoba, and Quebec (Peacock et al., 2010).

Western Hudson Bay Polar Bears The western HB polar bear population has been declining since 1981. The decline is believed to be caused by a lengthening of the ice free season (summer) which has led to increased nutritional stress (Stirling et al., 1999). The increased open water season is correlated with poor condition especially in female polar bears (Stirling et al., 1999). The population was estimated at 1200 bears based on an estimate from 1987 (Lunn et al., 2002), giving a biomass for the region of $0.00046\text{t}\cdot\text{km}^{-2}$. In 2004 the population is believed to have dropped to 935 animals (Aars et al., 2005).

An average catch of 44 bears during the 1980s (Lee and Taylor, 1994) has since increased slightly to 46.8 bears for the 1999-2004 period (Aars et al., 2005). The 2005 quota for the WHB polar bear population was 56 bears (Aars et al., 2005). Diet was set to 1% polar bears (Western Hudson Bay), 0.5% northern walrus, 12.5% bearded seals, 0.1% harbour seals, 61.9% ringed seals, 3% harp seals, 10% western beluga whales, 2% seabirds, 1% each echinoderms and bivalves, 7% other benthos.

Southern Hudson Bay Polar Bears The SHB polar bear population was estimated at 1000 bears in the 1980s (Lunn et al., 2002), giving a biomass of $0.000383\text{t}\cdot\text{km}^{-2}$ for the entire region. There have been no estimates of this population since, therefore the estimate of 1000 bears was used for the starting 1970s biomass. The diet for SHB polar bears was set to: 1% SHB polar Bears (to account for cannibalism), 0.5% southern walrus, 12.5% bearded seals, 0.1% harbor seals, 62.4% ringed seals, 3% harp seals, 0.5% eastern belugas, 6.5% James Bay belugas, 7% seabirds, 2% echinoderms, 2% bivalves, and 2.5% other benthos. The average catch of SHB polar bears for the 1980s was 68 (Lee and Taylor, 1994), and with no previous records available, this values was assumed to be the catch for 1970.

Foxe Basin Polar Bears The FB polar bear population has shown a decrease from 3000 bears (1970s) to 2100 (1996), and then a slight increase to 2300 in 2004 (Aars et al., 2005). This population is not fully within the model limits so the 1970s abundance would yield a biomass of $0.000986\text{t}\cdot\text{km}^{-2}$, however it was assumed only 20% of the population was geographically located within the model area, so the biomass was adjusted to $0.000197\text{t}\cdot\text{km}^{-2}$.

Average catches for the 1980s were 142 bears (Lee and Taylor, 1994). This value was used as the catch in 1970, although again it was also adjusted to 20% of its value to account for the percentage taken from within the model area. The diet for FB polar bears is believed to contain less birds and invertebrates and more seals (Russell, 1975) and was therefore set to 0.5% FB polar bears, 20% bearded seals, 1% harbor seals, 59.5% ringed seals, 4% harp seals, 8% western Belugas, 2% seabirds, 1.5% echinoderms, 1.5% bivalves, and 2% other benthos.

Killer Whales (*Orcinus orca*)

There has been an observed increase in the number of killer whales present in Hudson Bay since the 1950s which has been linked to the decreasing ice cover in the region (Higdon and Ferguson, 2009). Killer whales move into Hudson Bay through Hudson Strait in the summer when the ice has melted enough to allow them to travel through, and they leave before the annual freeze-up. It is believed they travel into the area following other marine mammal species as food, although a determined ecotype has not been established for these animals. Inuit knowledge suggests killer whales were not present prior to the mid-1900s but are now observed on a regular basis (Gonzalez, 2001). A photo identification project established in 2005 has identified 67 unique individuals in the Eastern Arctic (Peterson et al., 2009).

The 1970s population was set to 20 individuals or a biomass of $0.000025\text{t}\cdot\text{km}^{-2}$ based on the conservative population estimate for the 2000s of at least 67 individuals, and sightings which have increased nearly fivefold since

the 1970s (Higdon and Ferguson, 2009). Although killer whales only enter HB during the ice-free season, it was assumed that for the proportion of the population which do, they feed completely on the species in the model area. Therefore no adjustments to the biomass were made.

Reported observations of predation consist of marine mammals, although not enough research has been completed to identify this population of killer whales as marine mammal consumers. In addition, reports from killer whales in other areas of Canada have stated observations of whales eating fish (Lawson et al., 2007; Higdon and Ferguson, 2009). The diet was therefore set primarily to marine mammals with some fish and birds being consumed; 8% narwhal, 2.5% bowhead, 6% walrus (3% each north and south walrus), 13% bearded seal, 1.5% harbor seal, 33% ringed seal, 3% harp seal, 22% beluga (1% eastern, 16% western, 5% James Bay), 3% seabirds, 0.5% Atlantic Salmon, 3% gadiformes, 2% sculpins/zoracids, 0.5% sharks/rays, 1% other marine fish, and 1% cephalopods (Gonzalez, 2001; Higdon, 2007; Higdon and Ferguson, 2009).

Based on increased sightings in Higdon and Ferguson (2009) for Hudson and James Bays, sightings of killer whales was assumed to be directly proportional to the number of killer whales present. A review of literature by Higdon (2007) summarized reported kills of killer whales from 1957 onwards in the eastern Canadian Arctic. Since killer whales are occasionally harvested, hunting mortality for the first year was set intentionally low; to the equivalent of half the biomass of one whale to give a hunting mortality of 0.103y^{-1} . This combined with the natural mortality led to a P/B of 0.151y^{-1} to be used in the model.

Narwhal (*Monodon monoceros*)

The Northern Hudson Bay stock of narwhal is the smallest of three narwhal stocks (Northern Hudson Bay, Baffin Bay, and Greenland Sea) in the Arctic (COSEWIC, 2004a). Narwhals are found near the Repulse Bay area of Hudson Bay in the summer months, and migrate to the Labrador Sea for the winter, spending roughly half of the year within the HB model area.

Although the wintering area for the Hudson Bay stock and the Baffin Bay stock overlap, summer site fidelity indicates they are different stocks (Westdal et al., 2010).

The stock for Hudson Bay was estimated to be 1355 individuals in 1984 (Richard, 1991), however this analysis did not account for submerged animals during the sampling, and should be doubled (to 2710) to more accurately represent the population. An estimate of 1780 whales for the population in 2000, also under-representative due to diving animals was corrected to 3500 whales, which is believed to be a more accurate value (COSEWIC, 2004a). Biomass and catches were adjusted to 50% of original values to accommodate for time spent and feeding outside of the model area.

Narwhal diets in HB are thought to be focused on Arctic cod, squid, and crustaceans, also including demersal species and invertebrates (Heide-Jorgensen, 2002; COSEWIC, 2004a; Stewart and Lockhart, 2005). The diet was set to 1% Arctic char, 1% Atlantic salmon, 25% gadiformes, 15% sculpins/ zoarcids, 12% capelin, 10% other marine fish, 2% brackish fish, 10% cephalopods, 5% macro-zooplankton, 4% euphausiids, and 15% crustaceans.

Bowhead (*Balaena mysticetus*)

The eastern Canadian Arctic bowhead whales are one of two populations worldwide, with the other being in west Greenland. Previously the Canadian population was believed to be two stocks (George et al., 1999), although genetic sampling has shown not to support this idea suggesting whales are from the same stock (Ferguson, 2007). Bowheads are the largest marine mammals within the HB ecosystem, with weight estimates ranging from 54,000kg up to 68,000kg or higher for adult individuals (Rugh and Shelden, 2002; American Cetacean Society, 2004) and can live for over 200 years (George et al., 1999). They have been an important source of food for historic cultures located in Hudson Bay starting with the Thule near 1000 AD (Higdon, 2008). Annual migrations coincide with the ice-free season in HB, where whales move into HB around April to May and leave in September. Although the

population has been estimated to be as high as 625 individuals in the 1860s for the HB region, it had dropped as low as or lower than 100 individuals in the late 1800s to early 1900s due to commercial whaling. Since reaching a low in the early 1900s the population has increased with model estimates of 300-400 whales (Higdon 2008 unpublished data). Survey data put the recent HB portion of whales at a minimum of 75 (not accounting for submerged animals at the time of the study) while the Foxe Basin portion of the study identified to be between 256-284 (again not accounting for submerged animals) whales in 1994 (Cosens and Innes, 2000). These are now believed to be from the same stock with differing summering grounds, and some sex segregation with mostly cow calf pairs in HB (Higdon and Ferguson, 2010).

The historical model estimates the 1970s population to be 319 whales, and it was assumed that roughly 20% of this population will enter Hudson Bay, as based on a 1994 survey where there were 75 whales in HB and 284 in Hudson Strait observed (DFO, 1999), giving an estimate of 64 whales. The biomass was then set to $0.0109\text{t}\cdot\text{km}^{-2}$.

The diet of bowhead whales is believed to consist primarily of copepods and euphausiids with other zooplankton (mysids, gammarid amphipods) and benthic crustaceans being consumed (Lowry et al., 1987; Rugh and Shelden, 2002). The diet was set to 5% macro-zooplankton, 30% euphausiids, 45% copepods, 5% crustaceans, 1% other meso-zooplankton, 5% micro-zooplankton, 2% marine worms, 1% echinoderms, 1% bivalves, and 5% other benthos.

Atlantic Walrus (*Odobenus rosmarus*)

Walrus are year round inhabitants of HB, surviving the winter on the ice. They utilize the sea ice as a platform for breeding, and rely on polynyas in order to feed throughout the winter (Stirling, 1997; NAMMCO, 2005a). Two of the five recognized stocks of walrus are located partially or fully within HB; the south and east Hudson Bay stock which is completely contained in the model (referred to as Walrus South in the model), and the Hudson Bay-Davis Strait stock (referred to as Walrus North in the model) where the

lower portion of the range reaches into the northern part of the model area (DFO, 2002b; COSEWIC, 2006). See Stewart (2008) for stock delineations. There are no complete stock assessments for any of the four walrus stocks, however estimates are presented for each of the HB stocks (DFO, 2002b). These stocks were split into two functional groups as they are hunted by different communities, and have different dietary habits.

Walrus N The Walrus North species group represents the Hudson Bay-Davis Strait stock. This population has been estimated to contain 3000-4000 animals in the mid 1970s (Richard and Campbell, 1988). This estimate represented the population within the entire stock range. However a 1976 survey for the Southampton/ Coates Islands region of northern Hudson Bay estimated 2370 animals in this smaller area (Mansfield and St Aubin, 1991). The population within the model was set to 2500 animals, a conservative estimate, or $0.00274t \cdot km^{-2}$ to represent the animals found within the model area from this population.

The diet for these animals consists mainly of benthic invertebrates (bivalves, gastropods, holothurians, polychaetes, and brachiopods), with bivalves contributing to nearly half the diet by weight (Fisher and Stewart, 1997; Kastelein, 2002; Born et al., 2003). Within the model the diet was set to: 2% gadiformes, 1% sculpins/zoarcids, 3% other marine fish, 6% crustaceans, 10% marine worms, 25% echinoderms, 40% bivalves, 13% other benthos.

Walrus S The Walrus South functional group represents the south and eastern HB stock, which is completely contained within the model area. The population has been estimated to be roughly 410 animals in the late 1970s from surveys at 2 locations in southern HB (310 and 100 walruses), although the reliability of this estimate has been questioned (Richard and Campbell, 1988; COSEWIC, 2006). Due to lack of better estimates a value of 500 animals was used for the 1970s starting biomass. Although there are no complete surveys, hunters have reported fewer walruses being observed than in the past (DFO, 2002b), indicating a declining population. The biomass

was set to $0.001\text{t}\cdot\text{km}^{-2}$.

This stock has been shown to be feeding at higher trophic levels than the other walrus group through stable isotope analysis. While these walruses do still consume bivalves and other invertebrates, they are also feeding on ringed seals and occasionally bearded seals (Muir et al., 1995, 2000). The diet was set to 0.1% bearded seals, 3.9% ringed seals, 8% gadiformes, 1% sculpins/zoarcids, 5% other marine fish, 7% crustaceans, 10% marine worms, 15% echinoderms, 40% bivalves, 10% other benthos.

Bearded Seal (*Erignathus barbatus*)

Bearded seals are year round inhabitants, using the pack ice and sea ice to haul out. They tend to be found near polynyas or other areas with open access to the water during the winter, and generally inhabit areas with a depth of 200m or less for foraging (Angliss and Outlaw, 2006). There have been no studies to suggest there is more than one stock of bearded seals in HB, and although there is no estimate for all bearded seals in HB, surveys have been conducted for the western portion of HB. Lunn et al. (1997) estimated 12900 and 1980 bearded seals for the western portion of HB in 1994 and 1995 respectively based on aerial surveys. It is believed the conditions of the survey played a large role in the discrepancies between estimates. The population for the 1970s was set to 15000 bearded seals for the entire model area or $0.0037\text{t}\cdot\text{km}^{-2}$, slightly higher than the 1995 estimate. This was set as a conservative estimate for the entire region as there are no known trends for bearded seals, and the surveys did not cover the entire region. It is believed that there may be declines in the bearded seal population as they are a prey item for polar bears, and declining polar bears (Western HB and Foxe Basin) have been shown to be declining possibly because of decreased ringed and bearded seals (Lunn et al., 1997). Hunting of bearded seals is not regulated, with few studies on estimates of numbers hunted (see section A.2).

Bearded seals are benthic feeders with bivalves and crustaceans being the most abundant items in the diet, but fish contributing the highest percent of

weight (Smith, 1981; Finley and Evans, 1983). Shrimp are more important to newly weaned seals while adults diets are most likely focused on clams (Young et al., 2010). The diet was set to 3% Arctic char, 2% Atlantic salmon, 20% gadiformes, 5% sculpins/zoarcids, 17% capelin, 4% sandlance, 5% other marine fish, 2% brackish fish, 1% cephalopods, 1% macro-zooplankton, 25% crustaceans, 2% marine worms, 8% echinoderms, 5% other benthos.

Harbor Seal (*Phoca vitulina*)

Harbor seals in Hudson Bay are known to reside in the marine environment as well as lakes which drain into HB (Mansfield, 1967b; Smith et al., 1996). The lake seals are not thought to migrate into the marine environment, and are therefore excluded from the model. Although there are no estimates for harbor seals in Hudson Bay, freshwater populations have been estimated between 100-600 seals for specific regions such as Lacs des Loups Marins, Quebec (Smith and Lavigne, 1994). Harbor seals are thought to be one of the least abundant seals in HB therefore the abundance was set to 1000 seals or $0.001\text{t}\cdot\text{km}^{-2}$ (Ferguson pers. comm.).

The diet of harbor seals consists primarily of benthic fish, invertebrates, squid, and crustaceans (Bigg, 1981). For the model the diet was set to 10% gadiformes, 8% sculpins/zoarcids, 20% capelin, 20% sandlance, 10% other marine fish, 6% brackish fish, 2% cephalopods, 2% macro-zooplankton, 2% euphausiids, 10% crustaceans, 3% marine worms, 3% echinoderms, and 4% other benthos.

Ringed Seal (*Pusa hispida*)

Ringed seals are the most abundant seals with a year round distribution in HB. Tagging studies show their ability to travel around Hudson Bay in a matter of weeks. However, seals tagged within Hudson Bay have not been shown to leave the region during the duration of the tagging study (Luque and Ferguson, 2008). Because these seals have been shown to travel large distances around HB, all ringed seals in the model area were considered one stock. Recent studies estimated the population size at 73170 in 2007

and 33701 in 2008 for the western portion of HB (DFO, 2009a) representing only a small portion of the model area. Densities estimated varied from $0.97 \pm 0.06 \text{ seals} \cdot \text{km}^{-2}$ in 2007 to $0.49 \pm 0.04 \text{ seals} \cdot \text{km}^{-2}$ in 2008 for western HB ranging from Arviat to Churchill (Chambellant and Ferguson, 2009). If seals were distributed evenly throughout the area the population estimate would range between 450,000 and 900,000 seals. 1975 estimates from projected population at 61000 seals for James Bay and 455,000 from Hudson Bay (Smith, 1975). The population for the 1970s was set to 600,000 seals, or $0.0469 \text{t} \cdot \text{km}^{-2}$.

In general ringed seals feed primarily on Arctic cod and other pelagic fish along with amphipods (DFO, 2009a). In the Baffin Bay region the diet is dominated by Arctic cod and Polar cod (Holst et al., 2001), but in HB sandlance, euphausiids, and capelin are the most frequent (Chambellant, 2010). The diet for Hudson Bay was set to: 18% gadiformes, 10% sculpins/zoarcids, 20% capelin, 30% sandlance, 8% other marine fish, 2% cephalopods, 2% macro-zooplankton, 2% euphausiids, and 8% crustaceans.

Harp Seals (*Phoca groenlandica*)

Harp seals are the least abundant of the seal species found in Hudson Bay, although there are no estimates for the abundance in this region. They enter Hudson Bay through Hudson Strait after the break-up of ice in the summer from the Gulf of St Lawrence and southeastern Labrador and leave the area before the freeze up in the fall (Stewart and Lockhart, 2005). Population estimates for harp seals in Newfoundland in the 1970s were between 700,000 to 1.5 million (Lavigne, 1979), however in addition to summering in HB, many animals move to Lancaster Sound, Baffin Bay, Hudson Strait, or Foxe Basin (Mansfield, 1967a). For the model the population within HB was estimated to be 8,000 (Ferguson pers. comm.) or $0.001 \text{t} \cdot \text{km}^{-2}$.

The diet of harp seals from Hudson Strait consists primarily of capelin, and is likely to be similar to the diet of seals within Hudson Bay. Other fish and invertebrate species found from stomach contents were: Arctic cod, sculpin, flatfish, rock cod, mysids, crustaceans, decapods, and other inver-

tebrates (Beck et al., 1993). The diet was set to: 2% Atlantic salmon, 2% gadiformes, 1% sculpins/zoarcids, 86% capelin, 5% other marine fish, and 4% crustaceans.

Beluga (*Delphinapterus leucas*)

Stocks of beluga whales are not fully known for the Hudson Bay region. The North Atlantic Marine Mammal Commission suggests there are 6 groups of belugas within Hudson Bay (NAMMCO, 2005a), while genetic studies suggest there are most likely two or three (de March and Postma, 2003), based on where whales are hunted or spend a majority of their time. de March and Postma (2003) demonstrate that some belugas harvested from Sannikiluaq are genetically different from the eastern HB and western HB populations. In addition it is possible that belugas harvested from Churchill are also a different stock, although this was not confirmed through genetics. Tagging studies have identified mixing between these populations, making divisions more difficult (Richard and Orr unpublished manuscript as cited in Stewart and Lockhart 2005). For the model three functional groups of Belugas were created to represent all populations within Hudson Bay: Eastern HB Beluga, Western HB Beluga, and James Bay Beluga. Although mixing between these groups is not well known, for modeling purposes it was assumed there are three separate stocks. As belugas do not spend the winter in HB, the biomass and catches were adjusted to 50% to account for six months within the model area.

The general diet of belugas has been noted as consisting primarily of fish species (with pelagic fish being important), benthic invertebrates and squids (Pauly et al., 1998b). In the Beaufort sea belugas feed primarily of cod (Loseto et al., 2009), while west Greenland belugas consume squid, molluscs, and myctophids in addition to cod (Heide-Jorgensen and Teilmann, 1994). Other noted prey items include crustaceans, worms, and sculpins (Stewart and Lockhart, 2005), with capelin as an important component to the diet of eastern and James Bay belugas (Kelley et al., 2010).

Beluga East HB Belugas residing in eastern Hudson Bay are considered part of the Ungava and Hudson Bay stock, which is currently listed as endangered by COSEWIC (NAMMCO, 2005a). The eastern HB population winters in northern Labrador and makes its migration past Ungava Bay and down the eastern coast of HB to its summer location ranging from Kuujuaapik to Inukjuak (DFO, 2001). There appears to be a strong genetic basis for designating belugas of Eastern Hudson Bay as a separate population and increasingly good evidence that they contribute to the harvests in Nunavik communities as far as Ungava Bay (COSEWIC, 2004b).

Areal transect surveys have shown varying trends in the population (Gosselin, 2005; Gosselin et al., 2009), however the general trend from surveys and modeling is the population has declined from roughly 4000 whales in 1985 to 2000-3100 whales in 2008 (Hammill, 2001; Gosselin, 2005; NAMMCO, 2005a; Hammill et al., 2009). These declines are thought to be caused primarily by hunting, although noise pollution, river dams, and environmental pollution are also considered factors (DFO, 2008). This population was listed as threatened by COSEWIC in 1988, and elevated to endangered status in May 2004 (COSEWIC, 2004b). Inuit communities have noted many of the rivers previously utilized by belugas along Hudson Strait and eastern Hudson Bay are no longer used. They believe noise is keeping the whales further offshore in these areas (COSEWIC, 2004b).

The biomass for the 1970s population was set to $0.00207t \cdot km^{-2}$ or 2100 whales (4200 whales at 50% of the time in the model area). The diet was set to: 2% Atlantic salmon, 8% gadiformes, 10% sculpins, 10% capelin, 5% cephalopods, 2% brackish fish, 15% euphausiids, 8% copepods, 17% crustaceans, 8% marine worms, and 15% other benthos.

Beluga West HB The western Hudson Bay beluga population arrive through Hudson Strait to Churchill, Nelson, and the Seal river estuaries through the summer (COSEWIC, 2004b). This population appears to be relatively abundant, although surveys have been sporadic (i.e. 1987 and 2005). COSEWIC (2004b) has designated this population as special concern due to potential substantial removals by hunting throughout its range and

concerns with hydroelectric dams and shipping. Estimates show the population as stable. Earlier surveys in 1985 and 1987 estimated the population at 23000 and 25100 whales respectively, while not accounting for submerged animals at the time of the survey (COSEWIC, 2004b; NAMMCO, 2005a). A 2004 estimate of 57300 whales suggests the population has not changed, as the uncorrected number from this survey is similar to the uncorrected abundances from previous studies (Richard, 2005). The 2004 survey also identified an additional 1300 animals along the Ontario coast and 700 along northern HB, however it was not known what stock these whales belonged to. Little genetic testing has occurred on the western HB population as it has been assumed to be one large stable population (COSEWIC, 2004b; Luque and Ferguson, 2010). The population of WHB belugas was set to 25000 whales (50000 whales at 50% of the time in the model area) to yield a biomass of $0.0247 \text{ t} \cdot \text{km}^{-2}$.

In western Hudson Bay belugas feed on capelin (*Mallotus villosus*), river fish, marine worms and squids (Culik, 2004), with capelin as an import contribution to the diet (Kelley et al., 2010). WHB belugas were assumed to feed on a slightly higher diversity of zooplankton due to the increased abundance found in WHB based on zooplankton samples (Harvey et al., 2006). The diet was set to 5% Arctic char, 2% Atlantic salmon, 15% gadiformes, 3% sculpins/zoarcids, 20% capelin, 1% sandlance, 4% other marine fish, 4% brackish fish, 5% cephalopods, 1% macro-zooplankton, 10% euphausiids, 5% copepods, 10% crustaceans, 5% marine worms, and 10% other benthos.

Beluga James Bay It was assumed that the hunting on this population occurs primarily from Sanikiluaq as the whales hunted at this community have been shown to be different from the EHB belugas (de March and Postma, 2003). Currently it is not fully known if this population is a separate population or constant mixture of other populations, as they appear to be more closely genetically related to western HB belugas than eastern HB belugas (COSEWIC, 2004b), although closer to eastern HB in proximity. Traditional knowledge indicates that there are some whales which spend the winter in James Bay, however it is not known if this is due to ice entrapment

or not (Stewart and Lockhart, 2005). Whales either remain overwinter in James Bay or migrate from the Quebec coast of HB into James Bay, with some migration around the Belcher Islands (Richard and Orr (2003) unpublished data as cited in Stewart and Lockhart, 2004). Since 2004, eight belugas from James Bay have been fitted with satellite tags, and none have been shown to move into eastern HB (Hammill unpublished data cited in Gosselin et al., 2009).

For the model, the James Bay beluga will be treated as its own population, with hunting pressure occurring from the Sanikiluaq (Belcher Island) community, as no harvest occurs within James Bay (COSEWIC, 2004b). Derived estimates of whale abundance have increased from roughly 1842 whales in 1985 to 3141 whales in 1993 to 7901 whales in 2001 (Gosselin et al., 2002). Estimates are considered conservative as they do not account for submerged animals, or those beyond survey view (Stewart and Lockhart, 2005). This apparent increase in the population based on the 2001 survey is too high to be explained by population growth, and is believed to be an artifact of survey coverage, and seasonal movements (COSEWIC, 2004b). A 2004 estimate of 3998 whales was believed to be too uncertain to use for management (Gosselin, 2005). The model population was set to 1842 whales for the 1970s giving a biomass $0.00147t \cdot km^{-2}$. This estimate did not account for submerged animals, and should be doubled based on the correction factors of other beluga populations. However, assuming belugas spend 50% of their year in the model area, the abundance of 1842 was used as is for input. The diet is believed to be focused heavily on capelin for this population (Stewart and Lockhart, 2005) and was set to 1% Atlantic salmon, 5% gadiformes, 50% capelin, 5% cephalopods, 10% euphausiids, 5% copepods, 10% crustaceans, 5% marine worms, and 9% other benthos.

Seabirds

The group for birds includes all migratory and year round inhabitants. Most species arrive after the breakup of ice and leave before the freeze up, with a few exceptions of year round inhabitants (Stewart and Lockhart, 2005).

Some 133 species of birds are recorded to utilize the HB marine ecosystem (appendix C) which funnels southbound migrating birds into James Bay, where the coastal marshes are an important stopover for many species (Stewart and Lockhart, 2005).

Biomass for this group was estimated using bird counts from another Arctic area, the Chukchi Sea, Alaska, as Hudson Bay estimates were unavailable. The average number of birds from 1989-1991 in this region was 75 birds km^{-2} (Johnson et al., 1993). This coupled with the average weight of the bird species found with the Hudson bay area of 867g (Karpouzi, 2005), gave a biomass estimate of $0.065\text{t}\cdot\text{km}^{-2}$. A P/B value of 0.113y^{-1} was used for natural mortality, based on the seabird population in the Aleutian Islands (Heymans, 2005), although a hunting mortality for HB based on catches of 0.005y^{-1} was calculated. The combined P/B value of 0.118y^{-1} was too low for the model and had to be increased to 0.37y^{-1} in order to balance the model. The EE was set to 0.95, to let the model estimate Q/B.

Diet for this group, was based data provided by Karpouzi (2005), and was set to 2% seabirds, 3% Arctic char, 3% Atlantic salmon, 2% gadiformes, 3% sculpins/zoarcids, 15% capelin, 4% sandlance, 4% other marine fish, 10% brackish fish, 10% cephalopods, 12% macro-zooplankton, 5% euphausiids, 1% copepods, 1% other meso-zooplankton, 2% marine worms, 3% echinoderms, 10% bivalves, 5% other benthos, 5% pelagic detritus.

Thick-billed murres have been monitored at Coats Island (in northern HB just southeast of Southampton Island) since 1985, and have shown an annual average increase in population (roughly 1.7% per year). Similar trends for thick-billed murres have been reported at Digges Island (just east of Coats Island at the northern edge of the model area) up until 2000 when the population appears to have leveled off (Gaston et al., 2009a). For the same region glaucous gulls have declined up to 50% (unpublished data cited in Gaston et al., 2009a)). Near the Belcher Islands surveys show the mean number of gull nests declining by 50% since 1980 and slight declines of Arctic terns (only significant declines at 1 of 5 sites surveyed) (Gilchrist and Robertson, 1999).

The breeding of thick-billed murres has become earlier (6 days earlier

since 1980), which is believed to be due to an earlier breakup of sea ice (17 days earlier when comparing 1988 to 2007), however it is not believed that changes to breeding cycles will be able to keep up with changes in environmental cycles (Gaston et al., 2009b,a). The diet of thick-billed murres has demonstrated shifts from Arctic cod to capelin as shown in figure 2.3 (Gaston et al., 2003). Although local changes appear to have occurred, it is hard to extrapolate to all bird species from regional studies. No large scale increases or declines have been observed in HB that would apply to all bird species within this group, therefore no assumptions on trends has been made for this model.

Fish

Fish species were determined based on the species named present in Hudson Bay and/or James Bay in appendix 3 of Stewart and Lockhart (2005). Species listed were categorized based on life history; marine, brackish, estuarine, diadromous, anadromous, or semi-anadromous. However as the model is defined as the marine ecosystem only species listed as marine and some species defined as brackish were included in the model. There are ten groups of fish in the model, based primarily on familial traits and secondarily on life history characteristics. Species found in each functional group are listed in appendix D.1.

As no comprehensive surveys have yet been completed, biomass was estimated for all fish groups, utilizing the ability of Ecopath with Ecosim to solve for one unknown parameter for each functional group. Biomass for all fish groups was estimated by the model using the inputs of P/B, Q/B, EE, and the diets of other functional groups.

Total mortality was set to the sum of fishing mortality and natural mortality, with the natural mortality being calculated using the life history tool page in Fishbase (Froese and Pauley, 2008), which provides equation A.2, where M is the natural mortality, L_{∞} = the maximum length of the fish, and T is the temperature of the water (in °C) (Pauly, 1980; Froese and Pauley, 2008). As little information is known about fish in Hudson Bay,

A.1. Model Parameters by Functional Group

default values provide by Fishbase for L_{∞} were used. For temperature, both the average value provided for the species based on temperatures fish are normally found in (provided by Fishbase), and an average of 0.5°C were used and calculated values are presented in table A.3. The 0.5°C value was chosen as it is the average water temperature for this region from 1960-2006, based on a global database of ice and sea surface temperature (SST) combining real and estimated data to obtain these values (Rayner et al., 2003; BADC, 2010).

$$M = 10^{0.566 - 0.718 \cdot \log L_{\infty} + 0.02 \cdot T} \quad (\text{A.2})$$

Table A.2: Fishing mortality based on per capita consumption rate of $120\text{kg} \cdot \text{person} \cdot \text{year}^{-1}$.

Species group	% of total catch	Catches (Tonnes)	Hunting Mortality
Arctic Char	35	421.614	6.33E-04
Atlantic Salmon	1	12.046	3.90E-05
Gadiformes	20	240.923	2.67E-04
Sculpins/ Zoarcids	20	240.923	6.60E-04
Capelin	10	120.461	1.82E-04
Sandlance	3	36.138	6.15E-05
Sharks/Rays	0	0	0
Other Marine Fish	5	60.231	9.14E-05
Brackish Fish	2	24.092	3.97E-04

Values for natural mortality (eq. A.2), were created using fish from tropical and temperate habitats and often underestimates mortality for polar species (Pauly, 1980). Therefore, when considering all the species in group, higher values were generally chosen.

Fishing Mortality

Fishing Mortality is likely to occur on all fish species in HB, as subsistence fishing is common. Catches from commercial fishery attempts have proven to be small and financially unsustainable, therefore there are currently no commercial fisheries operating in the model area at present, with only a few brief attempts in the past (Stewart and Lockhart, 2005). The only recreational fishery that information is available for is for Arctic char from 1988-1997 through DFO harvest records (DFO, 1990, 1991, 1992, 1993, 1994,

1995, 1996, 1997). Subsistence mortality was estimated using a per capita use rate derived from values provided by various sources from 1970-2001 (Anonymous, 1979; Gamble, 1988; Fabijian and Usher, 2003) for the communities of Arviat, Paulatuk, and Inukjuaq as presented in (Booth and Watts, 2007). For fish a per capita consumption rate of 30-120kg·person·year⁻¹ was estimated for 1970. Underreporting is believed to occur, therefore the upper estimate of 120kg·person·year⁻¹ was believed to be more accurate.

Based on a population size of 10,033 (see fishing section for community population estimates) this would yield a total catch of 1204.6t of fish caught for subsistence hunting in 1970. This was divided among all fish groups except sharks and rays. Catch was divided among the different species groups based on sporadic community records of fish catches from 1975-1990 as presented in table 14-8 of Stewart and Lockhart (2005). The contributions of total catches by species group are presented in table A.2, and include the estimated hunting mortality.

Consumption rates were calculated using equation J.6 from Palomares and Pauly (1998):

$$\log \frac{Q}{B} = 7.964 - 0.204 \cdot \log W_{\infty} - 1.965T' + 0.532h + 0.398d \quad (\text{A.3})$$

where W_{∞} is the weight a fish would reach if it grew to it L_{∞} (the mean length of very old fish), T' is the mean temperature in Kelvin, expressed as $(1000/(C + 273.15))$ with C representing temperature in degrees Celsius. A is the aspect ratio of the caudal fin, h and d represent variables for feeding types; $h=1$ if the fish is herbivorous, $h=0$ if it consumes other food types, $d=1$ if the fish is a detritivore, $d=0$ if the fish consumes other food types. Again a temperature of 0.5°C was used based on the average temperature for this region.

The Ecotrophic Efficiency (EE) for all fish groups was set to 0.95 in order to allow the modeling program to estimate biomass parameters. Previous modeling indicates values close to one are widely used for mid trophic level groups, indicating most of the organisms are consumed within the food web

or from fishing, and relatively few die from old age (Christensen et al., 2005). The value 0.95 was chosen to assume 95% of the population will die from predation and fishing mortality, a commonly used value for EE (Christensen et al., 2005). Parameters calculated for all fish species are presented in table A.3.

Arctic Charr

The Arctic Charr (*Salvelinus alpinus*) group consists of only one species. Charr are anadromous, living primarily in marine waters (Stewart and Lockhart, 2005). Due to the locations and increased availability for a short time period while in HB and JB, charr are hunted by subsistence and recreational hunters (Stewart and Lockhart, 2005). Arctic charr in HB prey on amphipods, mysids, and fish (Stewart and Lockhart, 2005). In Labrador the diet consists of fish (capelin, sand lance, and various sculpins), mollusks, crustaceans, insects, and chaetognaths (Dempson et al., 2002). Diet for the model was set to: 1% Atlantic salmon, 1% gadiformes, 1% sculpins/zoarcids, 2% capelin, 2% sandlance, 2% Other Marine Fish, 2% Brackish Fish, 10% macro-zooplankton, 5% euphausiids, 31% copepods, 10% crustaceans, 10% other meso-zooplankton, 10% micro-zooplankton, 3% marine worms, 2% echinoderms, 3% other benthos, 4% primary production, 1% ice algae.

Atlantic Salmon

The Atlantic salmon group also consists of only one species *Salmo salar*, which utilizes the marine environment during the winter in HB, JB, and HS. Although this species is not common in HB and JB it is harvested as bycatch, and is more prevalent in the Ungava Bay area just outside of the model area (Stewart and Lockhart, 2005). Atlantic salmon is not known to be a major contributor to predator diets. Although region specific studies have not been done, in other areas juveniles prey on a range of invertebrates (mollusks, crustaceans, and small fish), while adults have been known to prey on fish (capelin, sandlance, and small cod) (Froese and Pauley, 2008). For the model the diet was set to: 1% Arctic char, 1% Atlantic salmon,

A.1. Model Parameters by Functional Group

Table A.3: Calculated input parameters for all fish groups within the model. NA indicates parameter could not be calculated due to missing information required for calculations.

Group	Species	Common Name	L_{∞}	Average Temp $^{\circ}\text{C}$	Mortality at Average Temp	M at 0.5°C	Q/B at 0.5°C
Arctic Char	<i>Salvelinus alpinus</i>	Arctic Char		1.5	0.1	0.1	1.7
Atlantic Salmon	<i>Salmo salar</i>	Atlantic Salmon	156	9	0.3	0.25	7.14
Gadiformes	<i>Arctogadus glacialis</i>	Polar cod	34	8	0.55	0.46	2.3
	<i>Boreogadus saida</i>	Arctic cod	31.3	1	0.31	0.3	2.5
	<i>Gadus ogac</i>	Greenland cod	79.5	1	0.22	0.22	1.3
Sculpins/ Zoarcids	<i>Gymnocanthus tricuspis</i>	Arctic staghorn	31.5	1	0.3	0.29	2.2
	<i>Icelus bicornis</i>	twohorn sculpin	16.6	1	0.51	0.5	3.6
	<i>Icelus spatula</i>	spatulate sculpin	22.1	3	0.35	0.33	3
	<i>Myoxocephalus quadricornis</i>	fourhorn sculpin	33.1	1	0.32	0.32	2.1
	<i>Myoxocephalus scorpioides</i>	Arctic sculpin	23.2	1	0.32	0.39	2.9
	<i>Myoxocephalus scorpius</i>	shorthorn sculpin	21.9	9.3	0.79	0.64	2.7
	<i>Triglops murrayi</i>	moustache sculpin	21.1	10	0.65	0.42	3.1
	<i>Triglops pingelli</i>	ribbed sculpin	27.3	10	0.35	0.28	3
	<i>Gymnelus viridis</i>	fish doctor	58.1	1	0.28	0.28	1.6
	<i>Lycodes pallidus</i>	pale eelpout	27.3	1	0.41	0.35	2.6
	<i>Lycodes reticulatus</i>	Arctic eelpout	37.6	1.3	0.3	0.28	2.2
Capelin	<i>Mallotus villosus</i>	capelin	16.9	4.3	0.85	0.78	3.9
Sandlance	<i>Ammodytes dubius</i>	northern sand lance	26.2	2	0.45	0.44	3.8
	<i>Ammodytes hexapterus</i>	stout sand lance	31.5	10	0.47	0.38	2.4
Sharks/Rays	<i>Somniosidae</i>	sleepers			0.04		0.5
	<i>Rajidae</i>	skates			0.18		2
Other Marine Fish	<i>Leptagonus decagonus</i>	alligator poacher	22.1	1	0.45	0.41	3
	<i>Ulcina olraki</i>	Atlantic alligatorfish	9.2	1	1.03	0.77	5.3
	<i>Cyclopterus lumpus</i>	lumpfish	55	5	0.19	0.17	1.3
	<i>Eumicrotremus derjugini</i>	leatherfin lumpsucker	NA				4.7
	<i>Eumicrotremus spinosus</i>	Atlantic spiny lumpsucker	NA				4
	<i>Careproctus reinhardtii</i>	sea tadpole	31.5	3	0.57	0.32	2.4
	<i>Liparis fabricii</i>	gelatinous snailfish	21.1	8	0.94	0.42	3.1
	<i>Liparis gibbus</i>	dusky snailfish	54	1	0.33	0.21	1.7
	<i>Liparis tunicatus</i>	kelp snailfish	16.9	1	0.98	0.49	3.5
	<i>Anisarchus medius</i>	stout eelblenny	31.5	1	0.26	0.32	2.4
	<i>Eumesogrammus praecisus</i>	fourline snake-blenny	23.2	1	0.35	0.39	2.9
	<i>Leptoclinus maculatus</i>	daubed shanny	21.1	1	0.38	0.42	3.1
	<i>Pholis fasciata</i>	banded gunnel	31.5	1	0.49	0.32	2.4
	<i>Clupea harengus</i>	Atlantic Herring	30.4	9	0.48	0.39	10.1
Brackish Fish	<i>Lumpenus fabricii</i>	slender eel-blenny	38.1	1	0.28	0.28	2.2
	<i>Stichaeus punctatus</i>	Arctic shanny	14.5	12	0.94	0.55	3.9
	<i>Hippoglossoides platessoides</i>	Canadian plaice	70.4	1.4	0.19	0.18	1.7

2% gadiformes, 2% sculpins/zoarcids, 5% capelin, 2% sandlance, 2% other marine fish, 3% brackish fish, 5% cephalopods, 15% macro-zooplankton, 8% euphausiids, 8% copepods, 18% crustaceans, 3% other meso-zooplankton, 15% micro-zooplankton, 7% primary production, and 3% ice algae.

Gadiformes

The Gadiformes group includes Arctic cod (*Boreogadus saida*), Greenland cod (*Gadus ogac*), and Polar cod (*Arctogadus glacialis*). These fish are important to the diets of many marine mammals in the area (see narwhal, ringed seal, harp seal, and beluga sections), although Arctic and Polar cod are more important to higher predators than Greenland cod. Arctic cod are believed to be declining, as their presence in the diet of thick-billed murre has declined since the 1980s (Gaston et al., 2003).

Greenland cod in northern HB are omnivorous feeding primarily on benthic species; crabs, amphipods, polychaetes, and crustaceans, with few species consuming them, while Arctic cod take mostly copepods, hyperiid amphipods, ice-associated crustacea, and other pelagic prey, and are more important to higher predators than Greenland cod (Mikhail and Welch, 1989). The diet for this group was set to 2% gadiformes, 5% capelin, 5% sandlance, 6% other marine fish, 3% crustaceans, 15% marine worms, 15% bivalves, 20% other benthos, 10% ice algae, and 4% ice detritus.

Sculpins/Zoarcids

Sculpins (Family: Cottidae) and zoarcids or eelpouts (Family: Zoarcidae) were combined to form one functional group and include: Arctic eelpout (*Lycodes reticulatus*), Arctic sculpin (*Myoxocephalus scorpioides*), Arctic staghorn (*Gymnocanthus tricuspis*), fish doctor (*Gymnelus viridis*), fourhorn sculpin (*Myoxocephalus quadricornis*), moustache sculpin (*Triglops murrai*), pale eelpout (*Lycodes pallidus*), ribbed sculpin (*Triglops pingelli*), shorthorn sculpin (*Myoxocephalus scorpius*), spatulate sculpin (*Icelus spatula*), and twohorn sculpin (*Icelus bicornis*). These two families were combined as nearly all members are small benthic fish found in shallow, mostly

coastal waters. Of the eelpout species, only the fish doctor has been noted as important to predators, namely cods and sculpins, while the importance of pale and Arctic eelpouts are unknown (Stewart and Lockhart, 2005). However, sculpins are consumed by cods, seabirds, seals, and other marine mammals, in addition to being caught for sport fishing occasionally (Stewart and Lockhart, 2005). The diets of these fish include plant materials, aquatic insects, crustaceans, benthic amphipods, polychaetes, bivalves, and detritus (Froese and Pauley, 2008). The diet was set to 2% sculpins/zoarcids, 5% capelin, 5% sandlance, 4% other marine fish, 7% crustaceans, 15% marine worms, 11% echinoderms, 15% bivalves, 20% other benthos, 6% ice algae, and 10% ice detritus.

Capelin

Capelin (*Mallotus villosus*) is a marine species with a circumpolar distribution in the Arctic, sometimes occurring in brackish or freshwater, and is often found in schools (Froese and Pauley, 2008). The population in HB is believed to be a surviving remainder from a warmer time period, likely the 1880s or earlier, with large swarms occurring in southern HB (Dunbar, 1983). The ecology of adult capelin in HB is not well known (Stewart and Lockhart, 2005), although they have been shown to be an important prey item to belugas, harp seals, and many bird species (Beck et al., 1993; Gaston et al., 2003; Loseto et al., 2009). Changes to the diets of thick-billed murres have identified a possible increase in capelin from 1980-2002 for birds located in the northern portion of HB (Gaston et al., 2003). The general diet of capelin is based on planktonic crustaceans, copepods, euphausiids, amphipods, marine worms, and small fishes (Froese and Pauley, 2008). For the model the diet was set to 15% macro-zooplankton, 20% euphausiids, 20% copepods, 10% crustaceans, 5% other meso-zooplankton, 10% micro-zooplankton, 15% pelagic production, and 5% pelagic detritus.

Sandlance

The sandlance group contains two species the northern sand lance (*Ammodytes dubius*) and the stout sand lance (*Ammodytes hexapterus*). Both species are small bottom dwelling fish which burrow in the sand and are important in the diets of forage fish, seabirds, and marine mammals (Stewart and Lockhart, 2005). Sandlance feed on zooplankton, primarily copepods, crustaceans, and worms (Froese and Pauley, 2008). The diet was set to 2% cephalopods, 5% macro-zooplankton, 15% euphausiids, 35% copepods, 5% crustaceans, 10% other meso-zooplankton, 15% micro-zooplankton 10% pelagic production, and 3% pelagic detritus.

Sharks/Rays

The Greenland shark (*Somniosus microcephalus*) and the thorny skate (*Amblyraja radiata*) are both bottom dwelling and likely very uncommon in HB and JB. The Greenland shark has been suggested to be present in HB, and the thorny skate is only noted to be found in James Bay, within the model area (Stewart and Lockhart, 2005). Both are probably rare in the area, and not likely to be a significant contribution to fish biomass in general. Skates consume small fish and benthic invertebrates, while the Greenland shark consumes fish, seals, whales, and birds (Stewart and Lockhart, 2005; Froese and Pauley, 2008). The diet was set to 1% narwhal, 1% bearded seal, 1% ringed seal, 1% harp seal, 5% Arctic char, 2% Atlantic salmon, 15% gadiformes, 15% sculpins/zoarcids, 5% capelin, 8% sandlance, 1% sharks/rays, 6% other marine fish, 4% brackish fish, 5% cephalopods, 5% macro-zooplankton, 1% euphausiids, 5% crustaceans, 5% marine worms, 10% echinoderms, 1% bivalves, and 3% other benthos.

Other Marine Fish

The other marine fish group includes herring (family: Clupeidae), poachers (family: Agonidae), lumpfishes (family: Cyclopteridae), shannies (family: Stichaeidae), and gunnels (family: Pholidae), Species include: alligator

poacher (*Leptagonus decagonus*), Atlantic alligatorfish (*Ulcina olriki*), Atlantic Herring (*Clupea harengus*), Atlantic spiny lumpsucker (*Eumicrotremus spinosus*), banded gunnel (*Pholis fasciata*), daubed shanny (*Leptoclinus maculatus*), dusky snailfish (*Liparis gibbus*), fourline snakeblenny (*Eumesogrammus praecisus*), gelatinous snailfish (*Liparis fabricii*), kelp snailfish (*Liparis tunicatus*), leatherfin lumpsucker (*Eumicrotremus derjugini*), lumpfish (*Cyclopterus lumpus*), sea tadpole (*Careproctus reinhardti*), and stout eelblenny (*Anisarchus medius*).

These fish are all small benthic fish that live near varied substratum (mud, sand, and rocks), with the exception of herring, which are predominantly pelagic and schooling living from the surface to 200m. These fish are prey items for cod, seabirds, seals, other fish and lumpfish are noted to be eaten by Greenland sharks (Stewart and Lockhart, 2005). Diets of these fish are focused on benthic and pelagic invertebrates, primarily crustaceans, polychaetes, clams, fish eggs, zooplankton, and herring have the ability to filter feed (Froese and Pauley, 2008). The diet was set to 2% capelin, 1% cephalopods, 5% macro-zooplankton, 2% euphausiids, 20% copepods, 20% crustaceans, 2% other meso-zooplankton, 5% micro-zooplankton, 6% marine worms, 5% bivalves, 5% other benthos, 10% pelagic production, 10% ice algae, and 7% pelagic detritus.

Brackish Water Fish

The brackish water group includes two species of shannies (family: Stichaeidae) which were considered to be brackish based; Arctic shanny (*Stichaeus punctatus*) and the slender eelblenny (*Lumpenus fabricii*) and one righteye flounder (family: Pleuronectidae), Canadian plaice (*Hippoglossoides platessoides*). Although all three of these species are found in inshore waters, they have been classified as brackish rather than marine and are consumed by larger marine fish and seabirds (Stewart and Lockhart, 2005). The diets consist of invertebrates; crustacean, worms, and clams, in addition to small fish and fish eggs (Froese and Pauley, 2008). The diet was set to 2% capelin, 2% sandlance, 2% brackish fish, 2% cephalopods, 17% macro-zooplankton, 5%

euphausiids, 5% copepods, 15% crustaceans, 5% other meso-zooplankton, 20% other meso-zooplankton, 2% marine worms, 2% echinoderms, 6% other benthos, 9% pelagic production, 1% ice algae, and 5% pelagic detritus.

Zooplankton

Sampling of zooplankton has occurred twice in the HB region, once with a survey by Harvey et al. (2001) to sample the eastern side of HB in 1993, starting in JB and moving northward up the coast and into Hudson Strait. The second survey conducted in 2003 spanned from west to east just above 60°N latitude (Harvey et al., 2006). Results from the surveys indicate higher zooplankton biomass on the western side compared to the eastern side of Hudson Bay, and increasing concentration as samples increased in latitude from James Bay up into Hudson Strait.

From the 1993 south to north survey (Harvey et al., 2001), biomass of samples ranged from 2.6 to 28.1g·m². Original samples were presented in dry weight (0.52 to 5.62 g · m²), but converted to wet weight using a conversion factor of 5 (DW:WW) for zooplankton (Cushing et al., 1958; Caufope and Heymans, 2005). Samples were dominated by copepods, euphausiids, cnidarians, amphipods, and chaetognaths indicating sampling of the meso and macro-zooplankton (chaetognaths fall into the macro-zooplankton, while most other species are smaller and fall into the meso-zooplankton spectrum).

The 2003 east to west survey (Harvey et al., 2006) identified meso-zooplankton, dominated by copepods, to have 3 times more biomass than macro-zooplankton in Hudson Bay. This ratio was higher in Hudson Strait and Foxe Basin, up to 10 times more meso-zooplankton. Of the zooplankton standing stock 5-17% of the abundance of zooplankton sampled was macro-zooplankton for the HB portion with the chaetognaths *Sagitta elegans* as the most abundant. Wet weight of macro- and meso-zooplankton ranged from 5-10g·m² for HB samples, although biomasses were higher for Hudson Strait, up to 20g·m² for macro-zooplankton, and 110g·m² for meso-zooplankton.

Cephalopods

While little is known about cephalopods in HB, they appear in the diets of predators; birds, seals, and some whale species. *Gonatus fabricii* is an important prey item in the diets of thick-billed murres, and is the only species recorded within the model area (Gerdiner and Dick, 2010). However, *Rossia moelleri* and other unidentified cephalopods have been recorded just outside the model area (Gerdiner and Dick, 2010) indicating a strong possibility more than one species is found within HB. This combined with the diets of predators led to the belief cephalopods are present within the model area, and were therefore included as a functional group.

The biomass for cephalopods was estimated by the model given other parameters. The P/B and Q/B of 2.55 and $6.9y^{-1}$ were taken from the cephalopod group in the 1979 Aleutian Island model (Heymans, 2005). However, these values were adjusted in the balancing of the model to 1.5 and $5y^{-1}$ for P/B and Q/B. The EE for this group was set to 0.95. Diet for cephalopods was set to 1% Arctic char, 1% Atlantic salmon, 5% gadiformes, 5% sculpins/zoarcids, 8% capelin, 8% sandlance, 1% other marine fish, 4% cephalopods, 18% macro-zooplankton, 4% euphausiids, 13% copepods, 10% crustaceans, 10% other meso-zooplankton, and 12% micro-zooplankton based on the diet of Antarctic cephalopods (Rodhouse and White, 1995; Jackson et al., 2002).

Macro-Zooplankton

The macro-zooplankton group includes all zooplankton species larger than 2mm. Chaetognaths (*sagita elegans*) were the most abundant species from sample taken in eastern HB in 1993, with hydromedusa (*Aeginopsis laurentii*) being the second most abundant, and numerous unidentified species (Harvey et al., 2006). Biomasses from the 2003 survey were reported between $5\text{-}10\text{g}\cdot\text{m}^2$. A value of $7.5\text{g}\cdot\text{m}^2$ or $\text{t}\cdot\text{km}^2$ was used for the biomass. P/B values of zooplankton larger than 1 mg WW for the Prince William Sound model ranged from 0.1 to $1.5y^{-1}$ depending on the season, and Q/B ratios ranged from 0.33 to $5y^{-1}$ (Okey and Pauly, 1999). P/B for HB was set to

$1y^{-1}$ and Q/B set to $3y^{-1}$ based on the values from Prince William Sound. Chaetognaths were the most abundant species in this group, with a diet focused on copepods (Tonnesson and Tiselius, 2005). Other members of this group were believed to prey upon smaller zooplankton and phytoplankton species. The diet was set to 6.5% euphausiids, 19% copepods, 2% crustaceans, 5% other meso-zooplankton, 30% micro-zooplankton, 22% pelagic production, 10.5% ice algae, and 5% pelagic detritus.

Euphausiids

Euphausiids show increasing contribution to the meso-zooplankton biomass moving south to north (Harvey et al., 2001). euphausiids consisted of *Thysanchoessa rachii* and other unidentified species. Based on the 1993 samples euphausiids contributed on average $2.14g \cdot m^{-2}$ or $t \cdot km^{-2}$ to the zooplankton biomass. The P/B for this group was set to $3y^{-1}$ based on a krill larva value of 4, and adult krill value of 1 from the Antarctic Peninsula ecosystem model (Efran and Pitcher, 2005). A P/Q ratio of 0.25 was assumed (Christensen et al., 2005), to allow the model to estimate both EE and Q/B. The diet was set to 1% macro-zooplankton, 0.1% euphausiids, 55.9% copepods, 1% crustaceans, 5% other meso-zooplankton, 10% micro-zooplankton, 15% pelagic production, 8% ice algae, and 4% pelagic detritus based on the diet of Antarctic euphausiids (Pakhomov et al., 1997; Cripps and Atkinson, 2000; Atkinson et al., 2002).

Copepods

Small copepods dominate the mesozooplankton biomass, up to 82% of total zooplankton biomass at on station in northern HB (Harvey et al., 2001). The average biomass over all stations sampled in 1993 was $4.015g \cdot m^{-2}$ or $t \cdot km^{-2}$, and thus was the biomass used for the model. Species include: *Acartia longiremis*, *Calanus glacialis*, *Calanus finmarchicus*, *Calanus hyperboreus*, *Centropages hamatus*, *Metridia longa*, and *Pseudocalanus spp.* as well as other unidentified species. P/B for the Prince William Sounds model copepod group was $5y^{-1}$ (Okey and Pauly, 1999). Other zooplankton groups

show higher P/B values ranging from 5.8 to $36.3y^{-1}$ for the Aleutian Islands (Heymans, 2005) or 10.7 to $24y^{-1}$ for the Kerguelen Islands (Pruvost et al., 2005). A P/B of $16y^{-1}$ was used for the HB model. A P/Q of 0.25 was assumed to give a Q/B value of $64y^{-1}$ when balancing the model. Copepods are primarily grazers, with a strong link to ice algae identified in HB (Runge and Ingram, 1987, 1991). Copepods have also been noted to consume other zooplankton species (Metz and Schnack-Schiel, 1995). The diet was set to 5% micro-zooplankton, 70% pelagic production, 20% ice algae, and 5% pelagic detritus.

Crustaceans

The crustacean group includes all benthic crustaceans and zooplankton crustaceans (with the exception of euphausiids and copepods). The benthic and planktonic species were combined due to lack of distinction in the diet for higher predators. For the planktonic species this includes various Isopoda, Ostracoda, Amphipoda, Decapoda, and Cirripedia. Biomass for the planktonic component was averaged to $1.05g \cdot m^2$ based on the 1993 survey. For the benthic component more species were identified (147 species compared to 5 identified for pelagic with many unknown) from Amphipoda, Cirripedia, Cumacea, Decapoda, Isopoda, Nebaliacea, Ostracoda, Pycnogonida, and Tanaidacea. In the Weddell Sea benthic Crustacea and Chelicerata contribute $0.45g \cdot m^2$ or $t \cdot km^2$ (Jarre-Teichmann et al., 1997). Although the contribution of benthic crustaceans is known in this area, it was estimated to be no more than the planktonic component. A biomass of $1.8g \cdot m^2$ was used for the model. P/B for various crustacean plankton for Prince William Sound ranged from $2-8y^{-1}$ (Okey and Pauly, 1999). P/B for benthos ranged from $0.7y^{-1}$ for benthic crustaceans in the Weddell Sea (Jarre-Teichmann et al., 1997) to $2.1y^{-1}$ for benthic invertebrates for the Aleutian Islands (Heymans, 2005). A P/B value of $3.6y^{-1}$ was used along with a P/Q ratio of 0.25 to give a Q/B ratio of $14.4y^{-1}$.

Antarctic amphipod diet consists primarily of detritus with some polychaetes, crustaceans, echinoderms and bryozoans (Dauby et al., 2001). In

HB amphipods can significantly reduce the inshore algal biomass suggesting their ability to consume large amounts of producers (Stewart and Lockhart, 2005). Benthic crustaceans were assumed to be primarily scavengers and carnivores. The diet was set to 1% euphausiids, 5% copepods, 0.5% crustaceans, 1% other meso-zooplankton, 1% micro-zooplankton, 5% marine worms, 5% echinoderms, 5% bivalves, 10% other benthos, 30% pelagic production, 16.5% ice algae, 10% ice detritus, and 10% pelagic detritus.

Other Meso-Zooplankton

The other meso-zooplankton group includes numerous unidentified species from the phyla Cnidarians, Annelida, Mollusca, and Urochordata. The average biomass for this group based on the 1993 survey was $1.21\text{g}\cdot\text{m}^2$. The P/B was set to 10y^{-1} based on overall zooplankton averages from the Prince William Sound model (Okey and Pauly, 1999). The P/Q was set to 0.25 to give a Q/B of 40y^{-1} . Global analysis of meso-zooplankton consumption on primary producers indicated that in less productive marine systems meso-zooplankton were more reliant on alternative food sources such as protozoans and other zooplankton (Calbert, 2001). For the HB region the diet was assumed to be 5% euphausiids, 10% copepods, 2% crustaceans, 1% other meso-zooplankton, 10% micro-zooplankton, 45% pelagic production, 22% ice algae, and 5% pelagic detritus.

Micro-Zooplankton

The micro-zooplankton group includes all zooplankton smaller than 0.2mm . Sampling is not likely to include these smaller species as the mesh size in the nets is expected to let the smaller plankton through. Therefore there are no estimates of biomass for this group. Other model values for small zooplankton in the Aleutian Islands show a P/B ratio of 36y^{-1} and a Q/B of 112y^{-1} (Heymans, 2005). Herbivorous zooplankton from the Kerguelen Islands were estimated to have a P/B of 24y^{-1} and a Q/B of 96y^{-1} (Pruvost et al., 2005). Okey and Pauly (1999) state a P/B of 15y^{-1} for small zooplankton in Prince William Sound. For the HB model the P/B was set

to the lower range of $15y^{-1}$ and a Q/B of $45y^{-1}$ was assumed. The EE for this group was set to 0.95. As micro-zooplankton are primarily grazers, although they have been noted to consume detritus in addition to ice algae in the winter months (Bathmann et al., 1993). The diet was set to 75% pelagic production, 17% ice algae, and 8% pelagic detritus.

Benthos

There are few benthic species in the intertidal zone, however, below the sea ice the most common invertebrates are echinoderms, sea spiders, polychaetes, sea spiders, and worms (Stewart and Lockhart, 2005). Various surveys of HB from 1953-1967 (Atkinsor and Wacasey, 1989) identify presence of certain benthic species, however they fail to indicate abundance. From this survey there were 76 species of annelids identified, 157 arthropods, 53 cnidarians, 83 molluscs, 1 nemertean, 4 porifera, and 4 sipunculans. For each location species were recorded indicating which groups were present at the most locations. Benthos were split into four groups: marine worms, echinoderms, bivalves, and other benthos, primarily based on the diets of higher trophic level groups and their diets. Due to the lack of information for these species groups, parameters from other models of similar regions were incorporated and used for the benthic species.

Parameter values of benthic invertebrates for other high latitude regions (Gulf of Alaska, Kerguelen Islands, and the Weddell Sea) are presented in table A.4. Of the models built for higher latitudes, the Weddell Sea model is most comparable to the HB region, as the Gulf of Alaska and Kerguelen Islands are more open, productive ecosystems, while the Weddell Sea has less mixing compared to the other two. Brey and Gerdes (1998) found community P/B ratio to increase from $0.18y^{-1}$ to $0.55y^{-1}$ as depth increases for the Weddell and Lazarev Seas (Antarctica). For all benthic groups biomass was estimated, using inputs for P/B, Q/B, and a value of 0.95 for the ecotrophic efficiency.

Table A.4: Comparison of parameters for benthic functional groups from high latitude Ecopath models. Biomass (B) is presented in $t \cdot km^{-2}$, production to biomass ratio (P/B) and consumption to biomass ratio (Q/B) are presented as an annual rate y^{-1} . NA indicates value was not available

Functional Group	Model Area	Model Year	B	P/B	Q/B	Reference
Epibenthic Carnivores	Gulf of Alaska	1963	35.601	2	17	Heymans (2005)
Benthic Invertebrates	Gulf of Alaska	1963	5.194	0.98	6.553	Heymans (2005)
Deep benthic omnivores	Kerguelen Is.	1987	30	3	10	Pruvost et al. (2005)
Shallow benthic omnivores	Kerguelen Is.	1987	3.1	2.1	10	Pruvost et al. (2005)
Shallow benthic carnivores	Kerguelen Is.	1987	8.7	2	10	Pruvost et al. (2005)
benthic mollusca	Weddell Sea	1980s	NA	0.3	1	Jarre-Teichmann et al. (1997)
Tunicata	Weddell Sea	1980s	2.8	0.3	1	Jarre-Teichmann et al. (1997)
Porifera	Weddell Sea	1980s	4.81	0.18	0.6	Jarre-Teichmann et al. (1997)
Hemichordata	Weddell Sea	1980s	6.26	0.3	2	Jarre-Teichmann et al. (1997)
Lophophora and Cnidaria	Weddell Sea	1980s	7.49	0.1	1	Jarre-Teichmann et al. (1997)
Benthic Crustacea and Chelicerata	Weddell Sea	1980s	0.45	0.7	3.5	Jarre-Teichmann et al. (1997)
Polychaeta and other worms	Weddell Sea	1980s	27.51	0.6	4	Jarre-Teichmann et al. (1997)
Echinoidea	Weddell Sea	1980s	0.54	0.07	0.233	Jarre-Teichmann et al. (1997)
Crinoidea	Weddell Sea	1980s	6.2	0.3	1	Jarre-Teichmann et al. (1997)
Ophiuroidea	Weddell Sea	1980s	24	0.173	0.577	Jarre-Teichmann et al. (1997)
Asteroidea	Weddell Sea	1980s	20.88	0.08	0.267	Jarre-Teichmann et al. (1997)
Holothuroidea	Weddell Sea	1980s	NA	0.2	1.1	Jarre-Teichmann et al. (1997)
Large Crabs	Newfoundland	1995-1997	0.232	0.3	1.2	Heymans (2003)
Small Crabs	Newfoundland	1995-1997	1.942	0.3	1.5	Heymans (2003)
Lobster	Newfoundland	1995-1997	0.003	0.38	4.42	Heymans (2003)
Shrimp	Newfoundland	1995-1997	1.859	1.45	9.667	Heymans (2003)
Echinoderms	Newfoundland	1995-1997	112.3	0.6	6.667	Heymans (2003)
Polychaetes	Newfoundland	1995-1997	10.5	2	22.222	Heymans (2003)
Bivalves	Newfoundland	1995-1997	42.1	0.57	6.333	Heymans (2003)
Other Benthic Invertebrates	Newfoundland	1995-1997	7.8	2.5	12.5	Heymans (2003)

Marine Worms

The marine worm functional group includes all phyla of worms; Nematoda (round worms), Phoronida (horseshoe worms), Priapulida (priapulid or penis worms), Sipuncula (peanut worms), and Annelida (bristle worms). P/B and Q/B values of 0.6 and $4y^{-1}$ respectively, were used based on the Weddell Sea model for the group "polychaetes and other worms" (Jarre-Teichmann et al., 1997), along with an EE of 0.95. Feeding types range from deposit feeders (Polychaetes) to trap feeders (Sipunculans) (Por and Bromley, 1974; Brock and Miller, 1999). The diet was set to 1% macro-zooplankton, 1% euphausiids, 3% copepods, 1% crustaceans, 2% other meso-zooplankton, 3% micro-zooplankton, 1% marine worms, 1% echinoderms, 10% other benthos, 4% pelagic production, 12% ice algae, and 61% ice detritus.

Echinoderms

The echinoderm functional group contains all species under the phylum Echinodermata, which includes the following classes: Asteroidea (Sea stars), Crinoidea (sea lillies), Echinoidea (sea urchins), Holothuroidea (sea cucumbers), and Ophiuroidea (brittle stars). The P/B and Q/B ratios were taken from all echinoderm groups in the Weddell Sea model and averaged to give 0.164 and $0.63y^{-1}$ (Jarre-Teichmann et al., 1997). However, these values were too low to balance the model, so they were increased to 0.3 and $1y^{-1}$ (P/B and Q/B) to the higher limits of this phylum for the Weddell Sea model (as the values for Crinoidea) to balance the model. The diet was set to 1% euphausiids, 2% copepods, 5% crustaceans, 1% other meso-zooplankton, 3% micro-zooplankton, 10% marine worms, 1% echinoderms, 10% bivalves, 15% other benthos, 3% pelagic production, 8% ice algae, and 41% ice detritus to account for a range of feeding modes. Sessile echinoderms rely on suspended particles, while more active echinoderms such as seastars are able to actively hunt prey and most likely feed on other benthic species in the region.

Bivalves

HB bivalves are from the class Pelecypoda (phylum Mollusca). This class was given its own functional group due to its importance to walrus, bearded seals, and fish. The P/B and Q/B values of $0.57y^{-1}$ and $6.33y^{-1}$ were taken from the Newfoundland model (Heymans, 2003) and used for the HB values. The EE was set to 0.95 and the biomass was estimated by the model. As suspension feeders, bivalves were assumed to prey on species likely to come in contact with them. The diet was set to 3% copepods, 5% other meso-zooplankton, 5% micro-zooplankton, 5% pelagic production, 12% ice algae, and 70% ice detritus.

Other Benthos

The other benthos group includes all other invertebrate species found within HB. Those which have been named by Atkinsor and Wacasey (1989) include molluscs (Scaphopods or tusk shells), porifera (sponges), Pycnogonida (Arthropod: sea spiders), Ascidiacea (sea squirts), Brachiopoda (lamp shells), Cnidarians; anthozoa and hydrozoa (anemones/corals and hydroids), Bryozoa (moss animals). Based on the benthic invertebrate groups from the Gulf of Alaska (Heymans, 2005), the shallow benthic omnivores from the Kerguelen Islands (Pruvost et al., 2005), and the other benthic invertebrates from Newfoundland (Heymans, 2003), the P/B was set to $2.5y^{-1}$, and the Q/B was set to $12.5y^{-1}$. The EE was set to 0.95 and the biomass was estimated for this group. A general diet was set to 1% macro-zooplankton, 1% other meso-zooplankton, 1% micro-zooplankton, 1% marine worms, 1% echinoderms, 1% bivalves, 1% other benthos, 5% pelagic production, 22% ice algae, and 66% ice detritus, as there are a variety of feeding types in this group.

Primary Production

Primary production in the model was split into two groups; pelagic production and ice algae. Pelagic production refers to the producers which bloom in the springtime in a seasonal pulse and are not generally available to the food

web the remainder of the year. The ice algae group represents the species which are frozen into the sea ice in the fall and are released when the sea ice melts. Many of the species frozen within the ice are accessible throughout the winter via brine channels in the ice. Numerous species of producers exist including: dinoflagellates, Prasinophytes, cryptophytes, chryophytes, centric diatoms, chlorophytes, flagellates, Prymnesiophytes, and pennate diatoms (Harvey et al., 1997). Two surveys of phytoplankton have been completed in HB; one in 1993 sampling from James Bay up the east coast of Hudson Bay into Hudson Strait (Harvey et al., 1997), and a second in 2003 running east to west through the middle of HB (Harvey et al., 2006). The first survey in 1993 yielded estimates of $0.36\text{-}133.5\text{t}\cdot\text{km}^2$ (based on chl a samples of $1.2\text{-}145\text{mg}\cdot\text{m}^2$), and the second survey estimated $7.5\text{-}75\text{t}\cdot\text{km}^2$ (based on chl a samples of $25\text{-}250\text{mg}\cdot\text{m}^2$)¹⁵.

Pelagic Production

Pelagic production was sampled at $0.33\text{-}129\text{t}\cdot\text{km}^2$ ($1.1\text{-}431\text{mgchl a}\cdot\text{m}^2$) in 1993 (Harvey et al., 1997), although this was during the ice free season, so a biomass of $8\text{t}\cdot\text{km}^2$ was assumed as the starting value. The EE was set to 0.8 to represent a 20% sinking rate to detritus, and the P/B ratio was estimated by the model.

Ice Algae

The ice algae contribution to primary production was sampled to be $0.03\text{-}4.2\text{t}\cdot\text{km}^2$ ($0.1\text{-}14\text{mgchl a}\cdot\text{m}^2$) in 1993 (Harvey et al., 1997), $0.003\text{-}6\text{t}\cdot\text{km}^2$ for values ranging 1978-1990 (Legendre et al., 1996), and $0.03\text{-}3.6\text{t}\cdot\text{km}^2$ in 1986 (Tremblay et al., 1989). The contribution is thought to be slightly higher at the start of the model in 1970, as the extent of sea ice has decreased since this time. Ice algal contribution to total production has been estimated at 25% in Hudson Bay (Legendre et al., 1996) and ranging from to 57% of

¹⁵Wet weight ($\text{t}\cdot\text{km}^2$) was calculated using the conversion $\text{chl a} = 1.5\%$ of ash free dry weight (AFDW) (Farabee, 2001), $1\text{g carbon} = 2\text{g AFDW}$ (Cauffope and Heymans, 2005), and $1\text{g C} = 9\text{g wet weight (WW)}$ (Pauly and Christensen, 1995)

all production in the central Arctic to 3% in surrounding sub-Arctic areas (Gosselin et al., 1997). Biomass of algae within the ice has reached levels of $0.6\text{gC}\cdot\text{m}^2$ in the Antarctic (Weddell Sea and Antarctic Peninsula) during spring and fall in the 1980s (Garrison and Buck, 1989), giving a biomass of $5.4\cdot\text{km}^2$ (Pauly and Christensen, 1995)¹⁶. The biomass for HB was set to $3.5\text{t}\cdot\text{km}^2$.

The EE for ice algae was set to 0.65, to account for the export of producers from the ice algae to ice detritus. Based on Tremblay et al. (1989), at least 20% of ice algal production during the spring was exported to the benthos, with 30% remaining in the pelagic zone, and another 50% thought to remain in the water column. As a yearly average, it was assumed that 45% of ice algae was exported to the ice detritus group, resulting in an EE of 0.65. The P/B was estimated by the model.

Detritus

Detrital biomasses was calculated using equation A.4 (Pauly et al., 1993):

$$\text{Log}_{10}D = -2.41 + 0.954\text{Log}_{10}PP + 0.863\text{Log}_{10}E \quad (\text{A.4})$$

where D is the standing stock of detritus (in $\text{gC} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$), PP is primary productivity (in $\text{gC} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$), and E is the euphotic depth (in meters).

Ice Detritus

In April the maximum ice thickness is 1.5m with over 85% of HB being covered in sea ice (Danielson, 1971). To calculate ice detritus an average euphotic depth of ice algae was assume to be 0.5m, combined with the ice algae biomass gave a ice detritus biomass of $0.009\text{t}\cdot\text{km}^2$.

¹⁶Using the conversion for phytoplankton where 1g C=1g wet weight

Pelagic Detritus

For the pelagic detritus group, a euphotic depth of 50m was used (Harvey et al., 1997), to give a value of $0.33\text{t}\cdot\text{km}^{-2}$.

A.2 Fisheries Input

In order to incorporate hunting and fishing pressure on various species, numerous "fisheries" were created within the model to account for catches within the first year (1970), which were then continued through the temporal simulations in Ecosim. Catches for the first year, and subsequent years are presented.

Western Hudson Bay Polar Bears

The average catch for the 1980s for WHB bears was 44 (Lee and Taylor, 1994), and then increased to an average of 46.8 bears from 1999-2004 (Aars et al., 2005). Catches were set to 44 from 1970-1998, 46.8 from 1999, and then 47 from 2005-2010 based on the 2005 quota of 47 (Aars et al., 2005). Initial catch for 1970 was set to 44 bears.

Southern Hudson Bay Polar Bears

The average catch of SHB polar bears for the 1980s was 68 (Lee and Taylor, 1994) and decreased to an average of 40.4 from 1999-2004 (Aars et al., 2005). Catch was assumed to be 68 bears per year from 1970-1990, and then decreased to 40.4 from 1991-2004. The annual quota in 2005 was set to 25 bears (Aars et al., 2005)). Catches from 2005-2010 were set to 25 bears. For 1970 the catch was set to 68 bears.

Foxe Basin Polar Bears

Average catches for the 1980s were 142 bears (Lee and Taylor, 1994) and decreased to an average of 97.4 for 1999-2004 (Aars et al., 2005). Catches were assumed to be 142 bears from 1970 to 1990, and then 97.4 bears each

year until 2005, where the quota was raised from 97 to 106. It was assumed 106 bears were harvested each year from 2005-2010. For modeling purposes, these values were reduced to 20% to reflect the adjustments in biomass regarding the population size within the model area, as 20% of the Foxe Basin population resides in the model area. For 1970 the catch was set to 28.4 bears.

Killer Whale Hunting

Table A.5: Known killer whales harvests in the eastern Canadian Arctic from Higdon (2007)

Year	Number of Whales Harvested
1978	1
1981	12
1995	1
2000	5

Killer whales are not generally targeted, however they are occasionally hunted in HB (Ferguson pers. comm.). Table A.5 identifies known harvests of killer whales in the eastern Canadian Arctic (Higdon, 2007). These values were used for the HB killer whale population as relative catches. For 1970, there were no reported catches, however a value was needed in the model. The equivalent biomass of $\frac{1}{4}$ of a whale was used as a starting value.

Narwhal Hunting

In general narwhals are hunted during their migration and through the summer months primarily by Repulse Bay, with some involvement from other communities; Chesterfield Inlet, Coral Harbour, Ranklin Inlet, Whale Cove, and Cape Dorset (DFO, 1998; Westdal et al., 2010). The annual quota for the communities within HB is currently listed at 112 whales per year.

Catches of narwhal by Repulse Bay are shown in figure A.1, not including the struck and loss rate. Catches for 1970 were set to 6 whales, the same value for 1978, which is the first year there were any recorded catches. Reported struck and loss rates range from 40% of total catch (Roberge and

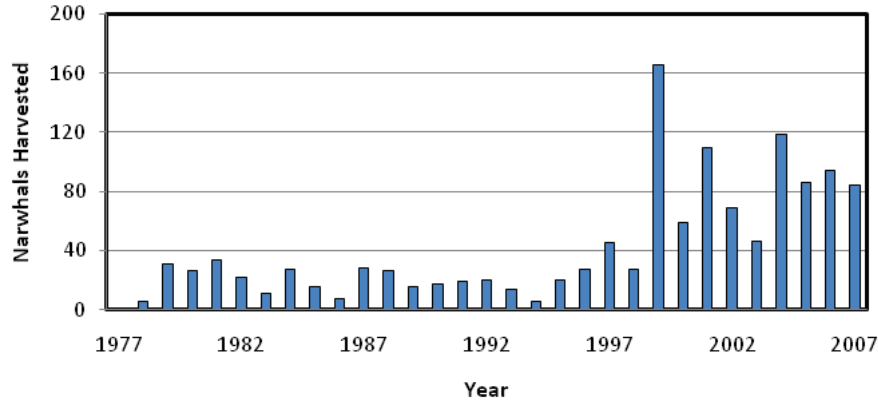


Figure A.1: Reported catches of narwhal from 1977-2007 for Repulse Bay, Chesterfiled Inlet, Coral Harbour, Ranklin Inlet, Whale Cove, and Cape Dorset (DFO, 1990, 1991, 1992, 1993, 1994, 1995, 1996, 1997; Stewart and Lockhart, 2005). Figure does not incorporate a struck and loss rate.

Dunn, 1990), to 12-56%, with specific hunts up to 71% (Weaver and Walker, 1988) as observed by the Department of Fisheries and Oceans (DFO). However, non-DFO observers of the hunt have commented on how hunters only take sure shots when being officially observed (Nicklen, 2007), meaning more whales are likely struck than the DFO statistics imply. The struck and loss term generally only accounts for whales known to die. Superficially wounded whales are not included in these estimates, even though they may not survive. Records also do not account for unreported catches.

Although the biomass was adjusted to 50% to account for half of the year (and feeding) to occur within the model area, as the catch data excludes the struck and loss rates, and underreporting. Catches were taken as is, without adjusting for the reduced biomass in the model, indicating mortality from catches is double than reported in figure A.1.

Bowhead Hunting

There have been 6 recorded kills of bowhead whales from the HB region; 1994 (unlicensed- Foxe Basin), 1996 (Repulse Bay), 1998 (Cumberland Sound),

2000 (Coral Harbour) 2003 (northern Foxe Basin), and 2005 (Repulse Bay) (Higdon, 2008). From 1918-1988 Inuit from Greenland and Canada killed an estimated 36 bowhead for harvest and another 14 were struck and lost (Higdon, 2008) since the end of commercial whaling, meaning of the 50 whales killed only 72% were harvested. In addition to the 6 recorded kills, a struck and loss rate of 25% was assumed (Ferguson pers. comm.) from 1994 onwards, meaning roughly 1 whale was killed every four years in addition to the 6 recorded kills. The catch for 1970 was set to 1 whale, with no catches until 1994 in the model.

Walrus Hunting

Hunting of walrus has been estimated at 35+ animals for south HB walrus and 230 for NHB walrus each year (NAMMCO, 2005a). However, reported landings are less than half of these estimated values. Hunting for southern walrus occurs in Sanikiluaq, Kuujjuarapik, Umiujaq, and Inukjuak while the Northern Walrus group incurs hunting pressure from Whale Cove, Rankin Inlet, Chesterfield Inlet, Repulse Bay, and Coral Harbour. Catches from 1972-1987 (Strong, 1989) and 1993-2003 from multiple sources summarized in (Stewart and Lockhart, 2005) were used to fit the model. Discrepancies between the two data sets stem from coverage of different communities.

Southern Walrus

For the southern walrus population, the 1972-1987 dataset only includes Sanikiluaq, were the 1993-2003 dataset also includes the communities Kuujjuarapik, Umiujaq, and Inukjuak, which almost certainly had catches for the earlier time period. The inclusion of more communities from 1993-2003 may artificially inflate hunting pressure within the model. However, despite the lack of more inclusive data from 1971-1987, the data is used "as is" and is used as relative catches to fit the model. Catches from 2004 onwards were set to the 2003 reported landings. The 1970 catch was set to 8 animals, the same as the catch in 1972, as there were no records of catches for 1970.

Northern Walrus

For the northern walrus population, the same 1971-1987 dataset includes catches from Whale Cove, Rankin Inlet, Chesterfield Inlet, Repulse Bay, and Coral Harbour. The latter dataset also includes Arviat, Ivujivik, Akulivik, and Puvirnituk. Again the catches were used as relative catches to fit the model. Catches from 2004 onwards were set to the reported value to 2003. Starting value for 1970 was 74 walrus, the same as the 1972 landings.

Beluga Hunting

All populations of beluga are hunted, however catch statistics do not distinguish between the stocks. Catches from western HB communities (Baker Lake, Chesterfield Inlet, Coral Harbour, Rankin Inlet, Repulse Bay, Sanikiluaq, and Whale Cove) were presumed to harvest the WHB beluga stock due to proximity. EHB and JB belugas are landed from communities on the eastern side of HB; Kuujjuarapik, Umiujaq, Inukjuak, Puvirnituk, Akulivik, and Ivujivik from Nunavik, and Sanikiluaq from Nunavut, as both groups migrate down the eastern coast of HB to their summering locations. Of the whales landed in Sanikiluaq (Belcher Islands), it was assumed that half were from the JB beluga group, and half were from the EHB beluga group, as tagging studies show eastern HB and JB belugas located around the Belcher Islands (de March and Postma, 2003). For the communities along the eastern coast of HB (Nunavik), the catches were thought to be mostly (70% of catches) from the EHB belugas, as the belugas not only using this as a migration route, but also summering in these areas. JB belugas use the same migration path, but move through to the summering location in James bay, making them available to hunters for a shorter period of time. The remaining 30% of catches from the Nunavik communities was determined to be from the JB beluga group. Catches from 2008-2010 were set to the 2007 value, for all groups. Figure A.2 identifies the trends in beluga harvest rates from 1970-2007 by stock, with landings per community taken from the Joint Commission on narwhal and beluga data (JCNB/NAMMCO, 2009).

As in the case with narwhals, a struck and loss rate was incorporated.

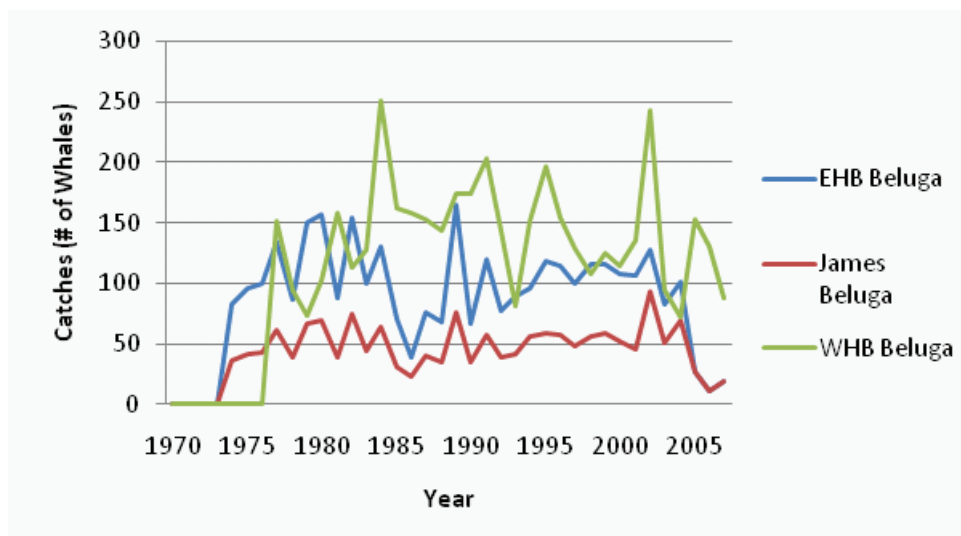


Figure A.2: Catches of beluga whales form 1970-2007 as aggregated by stock

Reports on 3 communities (1 within the model area) indicates mortality nearly 10 times higher than reported catches when struck and loss rates are considered. When considering loss rates from narwhal, this value appears high. However, as the biomass was adjusted to 50% to account for time within the model area, the catches were not. This assumes double the hunting mortality on all beluga stocks than is reported.

Beluga East

Catches for 1970 were set to the 1974 value of 83 whales, based on catches (JCNB/NAMMCO, 2009), and delineation of catches per community.

Beluga West

Catches for 1970 were set to the 1976 value of 152 whales.

Beluga James

Catches for 1970 were set to the 1974 value of 35 whales.

Sealing, Bird Hunting, and Fishing

In some cases catches were inferred based on a per capita basis, for many unregulated species. In these instances the increase in human population is used to calculate an increase in catches. Human community population size was used to estimate the harvest of birds, seals and fish. The human population in the Nunavut portion of Hudson Bay has more than doubled from 1981-2006, increasing from 4686 to 9491 inhabitants (Statistics Canada, 2006), however estimates before this are not available.

Using the data from 1981 to 2006, a linear regression was fit to the data to estimate the growth rate giving an R^2 value= 0.996 (figure A.3). The growth pattern was assumed to decline constant from the 1970-1981 time period, lacking better data. As community data for Nunavik was not as readily available, population growth was presumed to follow the same growth pattern as communities in Nunavut. In 2006 the total human population for all communities in HB (Nunavut and Nunavik) was 30,117 (Bell, 2002; Statistics Canada, 2006; Nunavut Bureau of Statistics, 2008; Sutherland et al., 2010). Following a linear decline in growth rate (figure A.3), this estimated the population to be 10,033 individuals for all Hudson Bay communities in 1970. This value was used to calculate hunting rates for seals, birds, and fish.

Sealing

Seal hunting is not currently regulated, although some estimates have been collected by community for 1975-1985 as summarized in table 14-9 various sources (Stewart and Lockhart, 2005). Based on the number of seals caught, species, and community population, a per capita hunting rate of $1.1 \text{ seals} \cdot \text{person} \cdot \text{year}^{-1}$ was used. Catches were broken down based on the number of each seal species killed, resulting in 92.6% ringed seals, 6.1% bearded seals, 1% harp seals, and 0.3% harbor seals. The total number of seals caught in 1970 was set to 9110. Number of people was used to drive effort of seal catches, with the proportion of each seal species remaining constant.

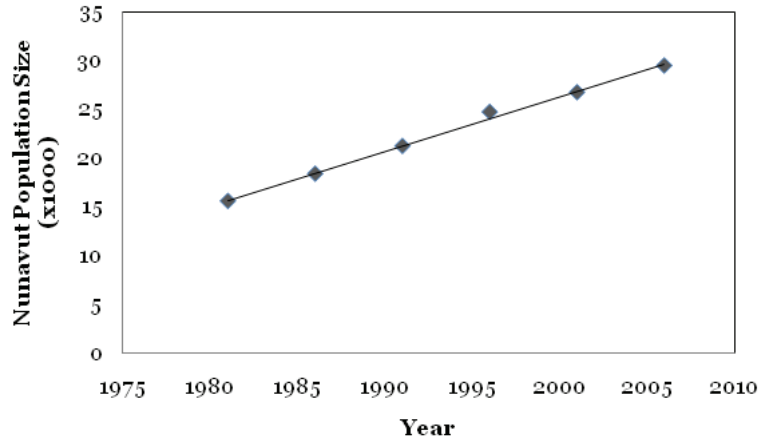


Figure A.3: Regression of community population size in Nunavut (all communities) from 1981-2006. Line represents model regression over data points.

Bird Hunting

Hunting of birds is not regulated and Inuit do not require a license. Birds, eggs, down and other inedible products can be harvested any time of the year by Cree or Inuit (Migratory Birds Convention Act, 1994). Based on survey records of bird harvests per community during 1975-1985 from table 14-10 (Stewart and Lockhart, 2005), it was estimated that an average of 21.3 birds were harvested for every member of the community. The catches for 1970 were set to 213,703 birds.

Fishing

Fishing rates were based on a per capita rate of $120\text{kg}\cdot\text{person}\cdot\text{year}^{-1}$. See Fishing mortality (table A.2 for breakdown of catches. Catches for 1970 were set to 1204 tonnes, with effort being driven by the number of people in the community.

A.3 Model Fitting Parameters and Data Sets

Time series data (table A.6) was read in as catches or abundance trends. For unregulated fisheries or hunting activities based on the size of the human population (fishing, bird hunting, and sealing), effort was driven by human population size (figure A.3).

Table A.6: Name and type of time series data used to fit the Hudson Bay Ecosim model

Data set	Type of Time series data
Bowhead Abundance	Relative Abundance
Bowhead Catches	Forced Catches
Foxe Basin Polar Bear Abundance	Relative Abundance
Foxe Basin Polar Bear Catches	Relative Catches
Western HB Polar Bear Abundance	Relative Abundance
Western HB Polar Bear Catches	Forced Catches
Southern HB Polar Bear Catches	Relative Abundance
Narwhal Catches	Forced Catches
Eastern HB Beluga Abundance	Relative Abundance
Eastern HB Beluga Catches	Forced Catches
Western HB Beluga Abundance	Relative Abundance
Western HB Beluga Catches	Forced Catches
James Bay Beluga Abundance	Relative Abundance
James Bay Beluga Catches	Forced Catches
Northern HB Walrus Catches	Forced Catches
Southern HB Walrus Catches	Forced Catches
Killer Whale Abundance	Forced Abundance
Killer Whale Catches	Forced Catches
Arctic Cod Abundance	Relative Abundance
Sculpin/Zoarcid Abundance	Relative Abundance
Capelin Abundance	Relative Abundance
Sandlance Abundance	Relative Abundance

Forcing Functions

The model is based on an understanding of the effects of climate change on the ecosystem. Warmer air temperatures, caused by climate change, have altered the mean ice freeze-up and break-up dates by 0.8-1.6 weeks in spring and fall (Hochheim et al., 2010). Figure 2.2 uses data from the HadISST (Hadley Centre Sea Ice and Sea Surface Temperature data set) model (BADC, 2010) to show the average % cover of sea ice for HB by month, with 95% CI. Starting in June, the variation in average ice cover increases, with June, July, November, and December having the greatest

variance in ice cover. The SST also becomes increasingly variable from June to December, and it is these changes in temperature and ice freeze-up and break-up dates that are thought to be important driver in the ecosystem and hence are implemented in the model. The availability of ice algae within the model is contingent upon the presence of sea ice, therefore the ice algae group was driven through a forcing function (FF) in the model. The sea ice FF was applied to the ice algae group, as a multiplier of the production rate using the average % cover of sea ice of all cells in the model area. The data was re-scaled to all positive values with a mean value of 1 for the first year (1970). The pelagic production functional group was also driven in the model through SST, using the same HadISST dataset. Figure 2.2 shows the annual SST average for HB by month, with 95% CI. Again, data was re-scaled to positive values with a mean value of 1 for 1970.

Mediation Functions

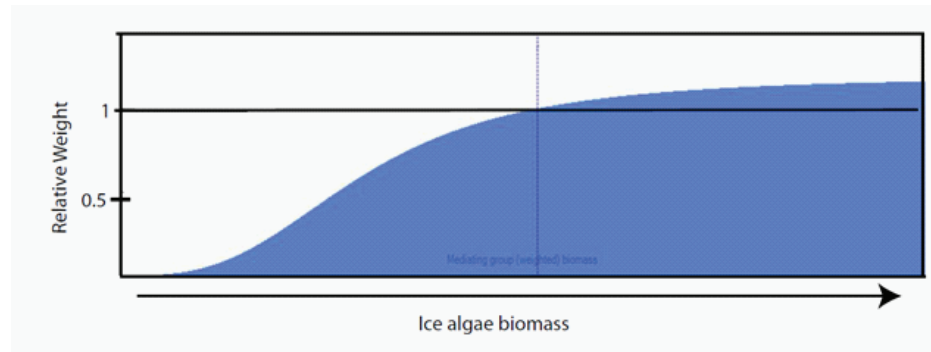


Figure A.4: Polar Bear Mediating Function with ice algae as the mediating group (x-axis). Y-axis shows the relative weight of polar bears, starting at $y=1$ (Ecopath value).

In order to fit the polar bear groups (FB, WHB, SH), a mediation function was used. Sea ice is critical to polar bear foraging, as they use the ice as a hunting surface (Stirling and Derocher, 1993). Declines in the western HB polar bear population from 1981-1998 have been linked to earlier breakup of the ice in the spring, and has been shown to cause reproductive stress

and decreased body condition (Stirling et al., 1999). These effects have only been shown to be significant for the western HB population, as the timing of sea ice break-up has changed only on the west coast of HB (Stirling et al., 1999; Stirling and Parkinson, 2006). A mediation function was applied to all polar bear groups, based on the changes in western HB. A sigmoid shape function was used with ice algae as the mediating group. As the biomass of ice algae increases (which is driven by the % sea ice cover, making it a proxy for sea ice), polar bears have a larger foraging area and their prey becomes more vulnerable to them. For the starting point, near the top of the curve was selected, as changes in the sea ice have been documented locally since the 1980s (Gaston et al., 2009b). The sigmoid shape was selected, as it is believed once the sea ice reaches a maximum/minimum, there is no added benefit/detriment to polar bears. The reference point on the curve which crosses the y-axis at 1 indicates the 1970 or starting value of the model, meaning increases in sea ice will have smaller effects on polar bears than decreases in sea ice.

Although declines in the Foxe Basin and southern HB populations of polar bears are not believed to be as extreme as WHB, it is highly likely they will respond to declines in sea ice the same way. Therefore the same mediation function was applied to all polar bear functional groups.

Biomass Accumulation

Abundance of Eastern HB belugas has declined from 1985-2008 (Hammill, 2001; Gosselin, 2005; Hammill et al., 2009), however the model was unable to capture this decreasing trend through hunting and predation alone. Moreover, the model was unable to capture the large increases in the JB beluga population. As the JB stock of belugas is genetically different from EHB belugas, it is hypothesized this stock is a constant mixture of other stocks (de March and Postma, 2003). Migration from EHB belugas to JB belugas was incorporated into the model in the form of biomass accumulation to assist in fitting. A decrease of $0.5\% \text{ y}^{-1}$ was necessary to fit the observed declines of EHB belugas. This led to an increased biomass accumulation of

1% y^{-1} to JB belugas, as the biomass of this group was roughly half the EHB biomass. Both P/B values were adjusted to accommodate for these changes; EHB beluga P/B was decreased from 0.0758 to 0.0658 y^{-1} , and JB beluga P/B was increased from 0.0673 y^{-1} to 0.0873 y^{-1} . A positive biomass accumulation rate was also used for bowhead whales, as the population is still rebounding from heavy commercial harvests (Higdon 2008 unpublished data), and the increases were not able to be captured by the model. A rate of 2% y^{-1} was initially used, however this value was later lowered to 0.7% y^{-1} , and was still able to capture the increase.

Group Info Parameters

The default maximum relative feeding time default of 2 was used for all species except marine mammals where it was set to 10 for all whale species (killer, narwhal, bowhead, and belugas), and 5 for all pinniped groups (walrus, harp, ringed, bearded, and harbor seals). The feeding time adjustment rate default of 0 was used for all species groups except marine mammals where it was set to 0.5 (Christensen et al., 2005, 2007).

Vulnerabilities

Vulnerabilities were first estimated using the automated fit to time series routine in Ecosim (Buszowski et al., 2009). Next, the vulnerabilities for individual predator prey interactions were adjusted to fit the model more accurately to time series data. All vulnerabilities are displayed in appendix E.

A.4 Model Parameterization and Output

Model Balancing

Many parameters were refined during the balancing process, through a series of steps. A general outline of the progression is presented, although adjustments to the diets were also made but not noted. Final parameter values

of the balanced model are presented in table A.7. The general processes of balancing the model follows.

- After creating all the functional groups and calculating general parameters, and diets, fishing groups were created. Once the catches for 1970 were determined, P/B ratios were adjusted to include hunting and fishing mortalities. After adjusting the P/B for marine mammals, birds, and fish, the P/B of fish had to be increased further.
- The equation used to calculate P/B for fish often underestimates higher latitude species (Pauly, 1980), and the smaller P/B was causing the model to estimate large biomasses of fish. Consequently, these ratios were increased to the upper limits based on the species found within the functional group.
- Many of the zooplankton groups lacked region specific data for P/B and Q/B, therefore a P/Q ratio of 0.25 was assumed, so the model could estimate an additional parameter.
- The EE of birds was too high indicating too much mortality. The P/B ratio was increased to allow enough hunting and predation mortality to occur in the model. Impacts of each functional group upon others are presented in appendix F, as output from the mixed trophic impact table in Ecopath.

Monte Carlo Simulations

Monte Carlo simulations were run using the pedigree ranking from Ecopath version 5 (Christensen et al., 2005). C.V. values were estimated based on quality of input data (see appendix G for all CV values and appendix H for graphs of biomass and P/B results). MC simulations were unable to improve the sum of squares value obtained by fitting the model. However, ranges of plausible ranges were obtained for biomass and P/B parameters. Biomass input CV and output with limits are presented in table A.8.

A.4. Model Parameterization and Output

Table A.7: Balanced Ecopath model with parameters estimated by the model in bold. Biomass is presented in ($t \cdot Km^{-2}$). Production/Biomass (P/B) and Consumption/Biomass (Q/B) are presented as an annual rate (y^{-1}). Trophic Level (TL), Ecotrophic Efficiency (EE) and Production/Consumption (P/Q) values are dimensionless.

Group name	TL	B	P/B	Q/B	EE	P/Q
WHB Polar Bear	4.857	0.0005	0.129	2.08	0.414	0.062
SH Polar Bear	4.906	0.0004	0.154	2.08	0.506	0.074
Polar Bear Foxe	4.927	0.0002	0.121	2.08	0.304	0.058
Killer Whale	4.872	0	0.151	4.998	0.265	0.03
Narwhal	4.062	0.0019	0.084	26.182	0.271	0.003
Bowhead	3.335	0.0109	0.021	5.475	0.384	0.004
Walrus N	3.332	0.0027	0.172	47.123	0.188	0.004
Walrus S	3.452	0.001	0.097	33.778	0.143	0.003
Bearded Seal	3.866	0.0037	0.176	14.262	0.791	0.012
Harbour Seal	3.971	0.001	0.125	18.612	0.074	0.007
Ringed Seal	4.077	0.0469	0.158	17.272	0.413	0.009
Harp seal	4.103	0.001	0.126	15.66	0.688	0.008
Beluga E	3.694	0.0021	0.066	21.448	0.22	0.003
Beluga W	3.873	0.0247	0.064	16.713	0.133	0.004
Beluga James	3.869	0.0015	0.087	16.623	0.679	0.005
Seabirds	3.839	0.065	0.37	17.258	0.95	0.021
Arctic Char	3.3	0.412	0.2	1.5	0.95	0.133
Atlantic Salmon	3.45	0.148	0.52	7.15	0.95	0.073
Gadiformes	3.235	0.853	0.47	1.85	0.95	0.254
Sculpins/ Zoarcids	3.188	0.382	0.7	3.269	0.95	0.214
Capelin	3.132	0.488	1.7	4.8	0.95	0.354
Sandlance	3.128	0.705	0.85	3.45	0.95	0.246
Sharks/Rays	4.033	3.18E-06	0.22	1.25	0.95	0.176
Other Marine Fish	2.948	0.374	0.932	3.018	0.95	0.309
Brackish Fish	3.216	0.055	3.5	5.798	0.95	0.604
Cephalopods	3.645	0.227	1.5	5	0.95	0.3
MacroZooplankton	2.711	7.5	1	3	0.278	0.333
Euphausiids	2.787	2.148	3.3	13.2	0.8	0.25
Copepods	2.05	4.015	16	64	0.472	0.25
Crustaceans	2.41	1.8	3.6	14.4	0.584	0.25
Other MesoZooplankton	2.336	1.21	10	40	0.556	0.25
MicroZooplankton	2	2.235	15	45	0.95	0.333
Marine Worms	2.275	5.93	0.6	4	0.95	0.15
Echinoderms	2.575	8.708	0.3	1	0.95	0.3
Bivalves	2.148	5.942	0.57	6.3	0.95	0.091
Other Benthos	2.091	3.139	2.5	12.5	0.95	0.2
Pelagic Production	1	8	46.865	-	0.8	-
Ice Algae	1	3.5	46.197	-	0.65	-
Ice Detritus	1	0.009	-	-	0.904	-
Detritus	1	0.33	-	-	0.224	-

A.4. Model Parameterization and Output

Table A.8: CV used for Monte Carlo estimates of biomass. Results show the mean biomass (B), along with the upper and lower limits of the 95% CI presented in $t \cdot km^{-2}$

	Functional Group	B (CV)	Lower Limit	Mean B	Upper Limit
1	Polar Bear WHB	0.15	0	0	0.001
2	SH Polar Bear	0.15	0	0	0
3	Polar Bear Foxe	0.15	0	0	0
4	Killer Whale	0.15	0	0	0
5	Narwhal	0.15	0.001	0.002	0.003
6	Bowhead	0.4	0.002	0.011	0.02
7	Walrus N	0.25	0.001	0.003	0.004
8	Walrus S	0.25	0	0.001	0.001
9	Bearded Seal	0.25	0.002	0.004	0.006
10	Harbour Seal	0.25	0.001	0.001	0.002
11	Ringed Seal	0.25	0.023	0.047	0.07
12	Harp seal	0.25	0.001	0.001	0.002
13	Beluga E	0.15	0.001	0.002	0.003
14	Beluga W	0.15	0.017	0.025	0.032
15	Beluga James	0.15	0.001	0.001	0.002
16	Seabirds	0.4	0.013	0.065	0.117
17	Arctic Char	0.1	0.329	0.412	0.494
18	Atlantic Salmon	0.1	0.118	0.148	0.177
19	Gadiformes	0.1	0.683	0.853	1.024
20	Sculpins/ Zoarcids	0.1	0.305	0.382	0.458
21	Capelin	0.1	0.39	0.488	0.585
22	Sandlance	0.1	0.564	0.705	0.846
23	Sharks/Rays	0.1	0	0	0
24	Other Marine Fish	0.1	0.3	0.374	0.449
25	Brackish Fish	0.1	0.044	0.055	0.066
26	Cephalopods	0.25	0.113	0.227	0.34
27	Macro-Zooplankton	0.25	3.75	7.5	11.25
28	Euphausiids	0.15	1.504	2.148	2.792
29	Copepods	0.15	2.811	4.015	5.22
30	Crustaceans	0.15	1.26	1.8	2.34
31	Other Meso-Zoopl.	0.15	0.847	1.21	1.573
32	Micro-Zooplankton	0.25	1.117	2.235	3.352
33	Marine Worms	0.1	4.744	5.93	7.115
34	Echinoderms	0.1	6.966	8.708	10.449
35	Bivalves	0.1	4.753	5.942	7.13
36	Other Benthos	0.1	2.511	3.139	3.767
37	Primary Production	0.15	5.6	8	10.4
38	Ice Algae	0.15	2.45	3.5	4.55

Most marine mammal biomass results remained quite close to the starting value. Ringed seals had the largest starting biomass of any marine mammal group, and also the highest upper limit or largest biomass which could be supported by the system, followed by WHB Bay beluga and bowhead whales. Ringed seals had a large uncertainty, as population sizes are not well known, however the model is able to support a large biomass of these seals. Within the model framework, bowheads have the potential to double the biomass and still be supported by the ecosystem.

Although there was high uncertainty with the biomass of fish groups, the ability of the system to sustain moderate biomasses of fish is an added discovery due to the understudied nature of fish within the ecosystem. While commercial fishing endeavors have not been profitable, it would be assumed the region has a conservative fish biomass. Compared to other ecosystem models, total fish biomass is lower than other systems of similar latitude. Total fish biomass of HB is $3.42\text{t}\cdot\text{km}^{-2}$ compared to $4.32\text{t}\cdot\text{km}^{-2}$ in the Antarctic Peninsula (Chapter 3), although the Antarctic is more productive, the dominant species is krill (*Euphausia superba*), and commercial fisheries operations in this region have also proved difficult.

Total zooplankton biomass of $18.91\text{t}\cdot\text{km}^{-2}$ appears to fall within the ranges of observed samples. Harvey et al. (2006), estimated macro and meso-zooplankton from $10\text{-}20\text{t}\cdot\text{km}^{-2}$ for central HB, while a few samples from Harvey et al. (2001) reached close to $50\text{t}\cdot\text{km}^{-2}$ in northern HB¹⁷. However these high values were obtained from late summer values, and are likely not representative of an annual value.

Ecosim Fitting

Results of time series fitting, including effort and mediation are presented in figure 2.5. While most trends were captured by the model, there were a few exceptions. Foxe Basin polar Bear catch was not forced due to the unknown portion of catches coming from within the model area. Therefore it was presented as a relative catch sequence. Although the values for the

¹⁷Biomass was $5.5\text{g}\cdot\text{m}^{-2}$ dry weight using a conversion of 9g WW=1g DW (Pauly and Christensen, 1995)

data and the model are not the same, the trend appears to be similar, with catches decreasing and leveling out by the late 1980s.

James Bay beluga abundance was not able to increase to levels as high as survey estimates. While migration from the EHB beluga group (through biomass accumulation) improved the fit for both EHB and James Bay belugas, the full magnitude of the increase was unable to be fully captured within the model. Data for fitting fish groups provided insight as to general trends of abundance, however the model was unable to simulate the extreme increase in capelin and sandlance populations, as well as the full decreases in gadiformes and sculpins/zoarcids.

Biomass accumulation was crucial to obtaining fits for bowhead and EHB belugas. Bowheads were unable to increase as rapidly within the model, starting at such a low biomass, and a low P/B. Conversely, a small decline in EHB belugas was created through hunting mortality and vulnerability settings, but was not fully captured until a negative biomass accumulation component was added.

All polar bear groups demonstrated stable population sizes with hunting pressure. Vulnerabilities were able to cause small increases or decreases in the populations, however, the addition of mediation increased the sensitivity of these groups to changes in sea ice as well as vulnerabilities of their prey. Once the mediation function was applied (to arena area and vulnerability of prey), all polar bear groups became highly sensitive to small changes in vulnerabilities.

Ecosim Output

Starting from the bottom of the food web, shifts caused by forcing functions can be identified. Figure A.5 identifies changes in the lowest trophic levels of the ecosystem, with declines in ice algae and ice detritus of nearly 10% each, and increases in pelagic production (26%), and pelagic detritus (33%). Since both the ice algae and the pelagic production groups were forced, these changes are not surprising.

Changes in the detritus and producers are propagated to the next trophic

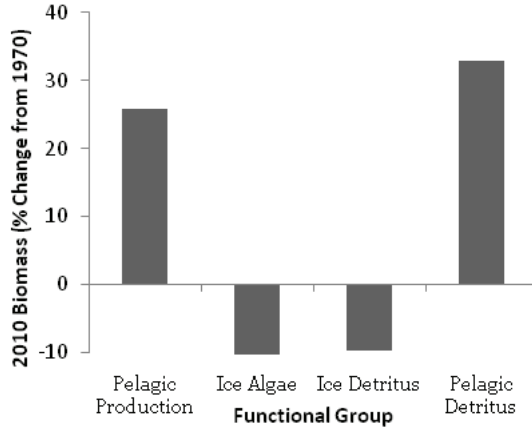


Figure A.5: Model end biomass for 2010 presented as percentage change from starting biomass for producers and detritus.

levels, as shown in figure A.6 by declines in all benthic groups, with the exception of crustaceans (although this group contains pelagic and benthic crustaceans). Zooplankton, however, fare much better, with increases ranging from 12% (micro-zooplankton) to 58% (macro-zooplankton). The increase in zooplankton is caused by the diets containing large concentrations of pelagic production, which supersede the declines in the ice algae contribution of the diet.

Declines are identified predominantly in benthic fish (Gadiformes: Arctic and Polar cod, Sculpins/Zoarcids: benthic fish, and sharks/rays) due to diets consisting of ice detritus and other benthos (figure A.7). Gadiformes and sculpins/zoarcids decreased in the diet of thick-billed murres an average of 68 and 57%, respectively (Gaston et al., 2003)¹⁸. Pelagic based fish show increases, with the largest being capelin and sandlance. Fitting of time-series data (figure 2.5) from the diet of thick-billed murres, appears to be unable to capture the full magnitude of the increase for both capelin and sandlance. Capelin increased in the diet from 20 to 50%, and sandlance from 4 to 20% (as averaged from the first and last 3 years). In the model

¹⁸When comparing the average contribution to the diet of thick billed murres as averaged over the first three and last three years of the diet study

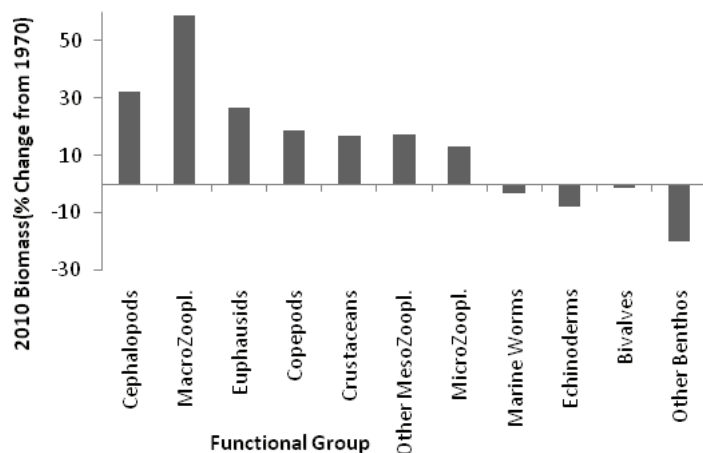


Figure A.6: Model ending biomass for 2010 presented as percentage change from the starting biomass for zooplankton and benthic groups

these groups show substantial increases with capelin increasing over 70% of their original biomass, with sandlance nearly doubling. Increased hunting and fishing pressure for birds and fish groups does not appear to be causing declines, as the mortality caused by hunting and fishing for these groups was quite small in relation to total mortality (table A.2). Seabird biomass was still able to increase within the model, despite hunting effort increasing roughly 4.5 times the 1970 effort.

Most marine mammal functional groups were fit to abundance data, therefore changes in biomass were previously known. All polar bear groups declined in biomass (figure A.8), primarily due to the mediation function hindering their ability to hunt effectively when there is less sea ice. Narwhal decreases are due to increasing hunting mortality. Biomass for narwhal remains relatively stable from 1970-2000. However, when catches are increased from 2000-2010, the population begins to decline, but only in the last 10 years of the simulation, indicating this is the result of hunting pressure (see narwhal graph in appendix I). Removal of catches in the model identifies an increase in narwhal biomass. Bearded seals also appear to decline due to hunting mortality (figure A.8). For bearded seals, hunting

A.4. Model Parameterization and Output

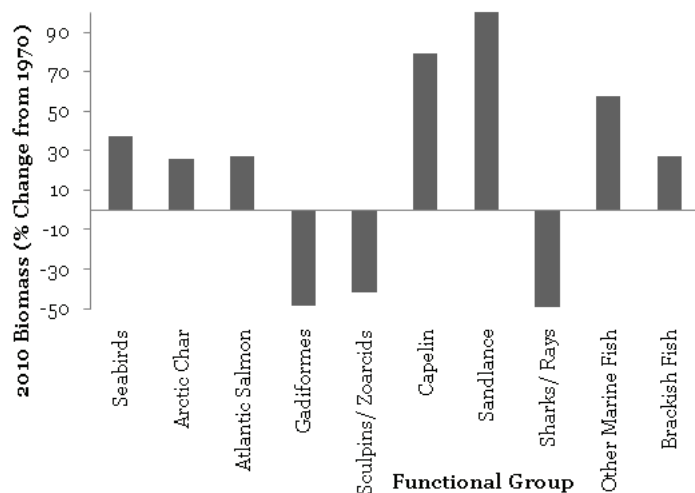


Figure A.7: Model ending biomass for 2010 presented as percentage change from starting biomass for fish and seabirds.

mortality accounts for one third of all mortality in Ecopath. Combined with the increases in human population and hunting pressure, by 2010 the hunting mortality is nearly 10 times the predation mortality indicating harvest of bearded seals is causing the decline within the model.

The harp seal group also shows hunting mortality to increase to double the predation mortality by the end of the simulation. However, because catches for this group were set low in the first year, large increases in catch are still unable to cause a decline overall. Ringed and harbor seals show low hunting mortality throughout the simulation, indicating the populations are large enough to sustain the effort levels used in the model fitting.

Both walrus groups (N and S) experience less predation from polar bears, due to declining populations. N walrus increase in the model due to low harvest levels from 2003-2010. S walrus experienced higher hunting pressure during this time, causing the decrease observed at the end of the model simulation.

Killer whale abundance was forced within the model to replicate the observed increase in killer whales. Biomass accumulation was unable to

A.4. Model Parameterization and Output

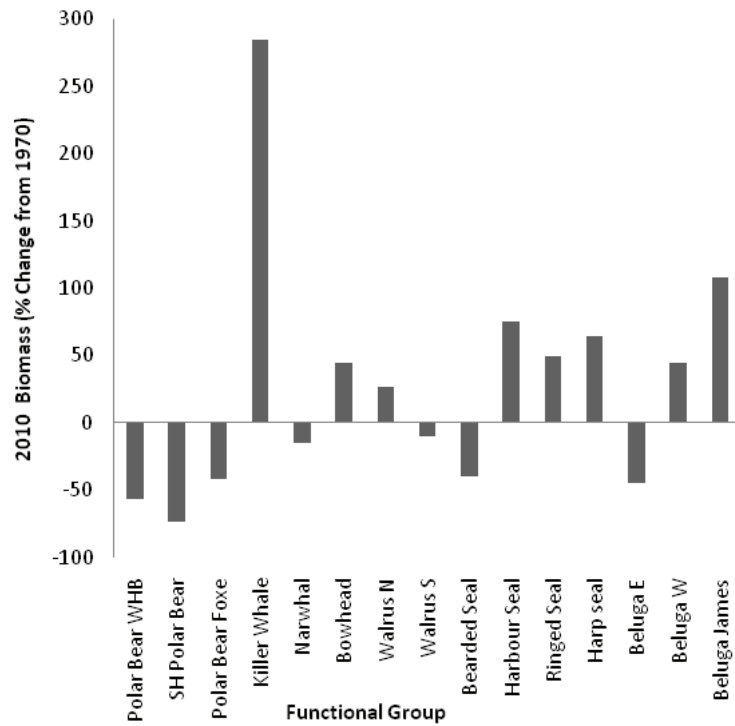


Figure A.8: Model ending biomass for 2010 presented as percentage change from starting biomass for marine mammal groups.

explain this large increase, leading the authors to believe the changes may be caused by immigration from other areas.

Appendix B

Marine Mammal Mortality Equations

Mortality for marine mammal functional groups was calculated based on life history information and estimates of longevity ($L(x)$), using equation B.1 to estimate the probability of survivorship from birth to age x , with information from equations B.2 to B.4, and parameters in table B.1.

$$L(x) = L_j(x) \cdot L_c(x) \cdot L_s(x) \quad (\text{B.1})$$

$$L_j(x) = \exp[(-a_1/b_1) \cdot 1 - \exp(-b \cdot x/\Omega)] \quad (\text{B.2})$$

$$L_c(x) = \exp[-a_2 \cdot x/\Omega] \quad (\text{B.3})$$

$$L_s(x) = \exp[a_3/b_3] \cdot 1 - \exp(b_3 \cdot x/\Omega) \quad (\text{B.4})$$

Where $L_j(x)$ is the mortality due to juvenile factors, $L_c(x)$ is the constant mortality experienced by all age classes, and $L_s(x)$ is the mortality due to senescent factors. Constant parameters $a_1, a_2, a_3, b_1, \text{ and } b_3$ allow flexibility in the shape of the survivor curve depending on life history traits of the species. For all pinniped groups survivorship curve parameters from northern fur seals were used to estimate survivorship (table B.1). Human survivorship parameter were used for killer whales and sperm whales, as there are few to zero predators on these groups, likely causing lowered juvenile mortality. Baleen whale (fin, minke, blue, humpback) survivorship was calculated using monkey and human survivorship parameters, however the monkey parameters were used as they had a slightly higher juvenile mortality. This was believed to be more representative of baleen whale sur-

Appendix B. Marine Mammal Mortality Equations

Table B.1: Marine mammal survivorship curve parameters based on life histories of fur seals, monkeys, and humans.

Species group	a_1	a_2	a_3	b_1	b_3
Northern Fur Seal	14.343	0.1710	0.0121	10.259	6.6878
Old World Monkeys	30.430	0.0000	0.7276	206.720	2.3188
Human (female)	40.409	0.4772	0.0047	310.360	8.0290

vivorship. Mortality was calculated as 1- the survivorship for each year of longevity, and averaged over all ages (x) to give the P/B value.

Appendix C

Hudson Bay Bird Species

Table C.1: Bird species found within the Hudson Bay model area by family, as reported from Stewart and Lockhart (2005). *Indicates the species is rare in its distribution within the model area.

Common Name	Species Name
Family Gaviidae: Loons	
red-throated loon	<i>Gavia stellata</i> (Pontoppidan, 1763)
Pacific loon	<i>G. pacifica</i> (Lawrence)
common loon	<i>G. immer</i> (Brnnich)
yellow-billed loon	<i>G. adamsii</i> (Gray)*
Family Podicipedidae: Grebes	
pied-billed grebe	<i>Podilymbus podiceps</i> (Linnaeus)*
horned grebe	<i>Podiceps auritus</i> (Linnaeus)
Family Procellariidae: Fulmars	
northern fulmar	<i>Fulmarus glacialis</i> (Linnaeus)*
Family Hydrobatidae: Storm-petrels	
Leach's storm-petrel	<i>Oceanodroma leucorhoa</i> (Viellot)*
Family Pelecanidae: Pelicans	
American white pelican	<i>Pelecanus erythrorhynchos</i> Gmelin*
Family Sulidae: Gannets	
northern gannet	<i>Sula bassanus</i> (Linnaeus)*
Family Phalacrocoracidae: Cormorants	
double crested cormorant	<i>Phalacrocorax auritus</i> (Lesson)
Family Ardeidae: Herons and Bitterns	
American bittern	<i>Botaurus lentiginosus</i> (Rackett)
great blue heron	<i>Ardea herodias</i> Linnaeus
snowy egret	<i>Egretta thula</i> (Molina)*
little blue heron	<i>E. caerulea</i> (Linnaeus)*
Continued on Next Page	

Appendix C. Hudson Bay Bird Species

Table C.1 Continued

Common Name	Species Name
tricolor heron	<i>E. tricolor</i> (Mller)*
black-crowned night heron	<i>Nycticorax nycticorax</i> (Linnaeus)*
Family Anatidae: Geese, Swans, and Ducks	
greater white-fronted goose	<i>Anser albifrons</i> (Scopoli)
snow goose	<i>Chen caerulescens</i> (Linnaeus)
Ross's goose	<i>C. rossii</i> (Cassin)
Canada goose	<i>Branta canadensis</i> (Linnaeus)
Brant	<i>B. bernicla</i> (Linnaeus)
trumpeter swan	<i>Cygnus buccinator</i> Richardson*
tundra swan	<i>C. columbianus</i> (Ord)
gadwall	<i>Anas strepera</i> Linnaeus*
Eurasian widgeon	<i>A. penelope</i> Linnaeus*
American widgeon (baldpate)	<i>A. americana</i> Gmelin
American black duck	<i>A. rubripes</i> Brewster
mallard	<i>A. platyrhynchos</i> Linnaeus
blue winged teal	<i>A. discors</i> Linnaeus
northern shoveler	<i>A. souchet</i> Linnaeus
northern pintail	<i>A. acuta</i> Linnaeus
green-winged teal	<i>A. crecca</i> Linnaeus
canvasback	<i>Aythya valisineria</i> (Wilson)*
redhead	<i>A. americana</i> (Eyton)*
ring-necked duck	<i>A. collaris</i> (Donovan)
greater scaup	<i>A. marila</i> (Linnaeus)
lesser scaup	<i>A. affinis</i> (Eyton)
king eider	<i>Somateria spectabilis</i> (Linnaeus)
common eider	<i>S. mollissima</i> (Linnaeus)
harlequin ducks	<i>Histrionicus histrionicus</i> (Linnaeus)
surf scoter	<i>Melanitta perspicillata</i> (Linnaeus)
white-winged scoter	<i>M. fusca</i> (Linnaeus)
black scoter (common scoter)	<i>M. nigra</i> (Linnaeus)
long-tailed duck (oldsquaw)	<i>Clangula hyemalis</i> (Linnaeus)
bufflehead	<i>Bucephala albeola</i> (Linnaeus)*
common goldeneye	<i>B. clangula</i> (Linnaeus)
Barrow's goldeneye	<i>B. islandica</i> (Gmelin)*
hooded merganser	<i>Lophodytes cucullatus</i> (Linnaeus)*
common merganser	<i>Mergus merganser</i> Linnaeus
red-breasted merganser	<i>M. serrator</i> Linnaeus
ruddy duck	<i>Oxyura jamaicensis</i> (Gmelin)*
Family Accipiteridae: Ospreys, Eagles, Hawks, and Allies	
osprey	<i>Pandion haliaetus</i> (Linnaeus)
bald eagle	<i>Haliaeetus leucocephalus</i> (Linnaeus)
northern harrier (marsh hawk)	<i>Circus cyaneus</i> (Linnaeus)

Continued on Next Page

Appendix C. Hudson Bay Bird Species

Table C.1 Continued

Common Name	Species Name
northern goshawk	<i>Accipiter gentilis</i> (Wilson)*
sharp-shinned hawk	<i>A. striatus</i> Vieillot
rough-legged hawk	<i>Buteo lapopus</i> (Gmelin)
golden eagle	<i>Aquila chrysaetos</i> (Linnaeus)*
Family Falconidae: Falcons	
merlin	<i>Falco columbarius</i> Linnaeus
peregrine falcon	<i>F. peregrinus</i> Tunstall
gyrfalcon	<i>F. rusticolus</i> Linnaeus
prairie falcon	<i>F. mexicanus</i> Schlegel*
Family Rallidae: Rails, Gallinules, and Coots	
yellow rail	<i>Coturnicops noveboracensis</i> (Gmelin)
sora	<i>Porzana carolina</i> (Linnaeus)
American coot	<i>Fulica americana</i> Gmelin
Family Gruidae: Cranes	
sandhill crane	<i>Grus canadensis</i> (Linnaeus)
Family Charadriidae: Plovers	
black-bellied plover	<i>Pluvialis squatarola</i> (Linnaeus)
American golden-plover	<i>P. dominica</i> (Muller)
semipalmated plover	<i>Charadrius semipalmatus</i> Bonaparte
killdeer	<i>C. vociferus</i> Linnaeus
Family Scolopacidae: Sandpipers, Phalaropes, and allies	
greater yellowlegs	<i>Tringa melanoleuca</i> (Gmelin)
lesser yellowlegs	<i>T. flavipes</i> (Gmelin)
solitary sandpiper	<i>T. solitaire</i> Wilson
spotted sandpiper	<i>Actitis macularia</i> (Linnaeus)
whimbrel	<i>Numenius phaeopus</i> (Linnaeus)
Hudsonian godwit	<i>Limosa haemastica</i> (Linnaeus)
marbled godwit	<i>L. fedoa</i> (Linnaeus)
ruddy turnstone	<i>Arenaria interpres</i> (Linnaeus)
red knot	<i>Calidris canutus</i> (Linnaeus)
sanderling	<i>C. alba</i> (Pallas)
semipalmated sandpiper	<i>C. pusilla</i> (Linnaeus)
little stint	<i>C. minuta</i> (Leisler)*
least sandpiper	<i>C. minutilla</i> (Vieillot)
white-rumped sandpiper	<i>C. fuscicollis</i> (Vieillot)
Baird's sandpiper	<i>C. bairdii</i> (Coues)
pectoral sandpiper	<i>C. melanotos</i> (Vieillot)
purple sandpiper	<i>C. maritima</i> (Brunnich)
dunlin	<i>C. alpina</i> (Linnaeus)

Continued on Next Page

Appendix C. Hudson Bay Bird Species

Table C.1 Continued

Common Name	Species Name
stilt sandpiper	<i>C. himantopus</i> (Bonaparte)
buff-breasted sandpiper	<i>Tryngites subruficollis</i> (Vieillot)
short-billed dowitcher	<i>Limnodromus griseus</i> (Gmelin)
Wilson's snipe	<i>Gallinago delicata</i> Ord
Wilson's phalarope	<i>Phalaropus tricolor</i> (Vieillot)
red-necked/northern phalarope	<i>P. lobatus</i> (Linnaeus)
red phalarope	<i>P. fulicaria</i> (Linnaeus)
Family Laridae: Jaegers, Gulls, and Terns	
Pomeranian jaeger	<i>Stercorarius pomarinus</i> (Temminck)
parasitic jaeger	<i>S. parasiticus</i> (Linnaeus)
long-tailed jaeger	<i>S. longicaudus</i> Vieillot
laughing gull	<i>Larus atricilla</i> Linnaeus*
Franklin's gull	<i>L. pipixcan</i> Wagler*
little gull	<i>Larus minutus</i> Pallas
black-headed gull	<i>L. ridibundus</i> Linnaeus*
Bonaparte's gull	<i>L. philadelphia</i> (Ord)
mew gull	<i>L. canus</i> Linnaeus*
ring-billed gull	<i>L. delawarensis</i> Ord
California gull	<i>L. californicus</i> Lawrence*
herring gull	<i>L. argentatus</i> Pontoppidan
Iceland gull	<i>L. glaucoides</i> Meyer
lesser black-backed gull	<i>L. fuscus</i> Linnaeus*
glaucous -winged gull	<i>L. glaucescens</i> Naumann*
glaucous gull	<i>L. hyperboreus</i> Gunnerus
great black-backed gull	<i>L. marinus</i> Linnaeus*
black-legged kittiwake	<i>Rissa tridactyle</i> (Linnaeus)
Ross's gull ¹¹	<i>Rodostethia rosea</i> (MacGillivray)
Sabine's gull	<i>Xema sabini</i> (Sabine)
ivory gull ¹²	<i>Pagophila eburnea</i> (Phipps)*
Caspian tern	<i>Sterna caspia</i> Pallas
common tern	<i>S. hirundo</i> Linnaeus
Arctic tern	<i>S. parasisaea</i> Pontoppidan
Forster's tern	<i>S. forsteri</i> Nuttall*
white-winged tern	<i>Chlidonias leucopterus</i> (Temminck)*
black tern	<i>C. niger</i> (Linnaeus)
Family Alcidae: Auks, Murres, and Puffins	
Dovekie	<i>Alle alle</i> (Linnaeus)
thick-billed murre	<i>Uria lomvia</i> (Linnaeus)
black guillemot	<i>Cephus grylle</i> (Linnaeus)
Family Strigidae: Typical owls	
snowy owl	<i>Nyctea scandiaca</i> (Linnaeus)

Continued on Next Page

Appendix C. Hudson Bay Bird Species

Table C.1 Continued

Common Name	Species Name
short-eared owl	<i>Asio flammeus</i> (Pontoppidan)
Family Alcedinidae: Kingfishers	
belted kingfisher	<i>Ceryle alcyon</i> (Linnaeus)
Family Corvidae: Crows and Ravens	
American crow	<i>Corvus brachyrhynchos</i> Brehm
common raven	<i>C. corax</i> Linnaeus
Family Alaudidae: Larks	
horned lark	<i>Eremophila alpestris</i>
Family Motacillidae: Pipits	
American pipit	<i>Anthus rubescens</i> (Tunstall)

Appendix D

Hudson Bay Fish Species

Table D.1: Fish functional groups and species included in each group.

Common Name	Species Name
Arctic Char:	
Arctic Char	<i>Salvelinus alpinus</i>
Atlantic Salmon:	
Atlantic Salmon	<i>Salmo salar</i>
Gadiformes:	
polar cod	<i>Arctogadus glacialis</i>
Arctic cod	<i>Boreogadus saida</i>
Greenland cod	<i>Gadus ogac</i>
Sculpins/ Zoarcids:	
Arctic staghorn	<i>Gymnocanthus tricuspis</i>
twohorn sculpin	<i>Icelus bicornis</i>
spatulate sculpin	<i>Icelus spatula</i>
fourhorn sculpin	<i>Myoxocephalus quadricornis</i>
Arctic sculpin	<i>Myoxocephalus scorpioides</i>
shorthorn sculpin	<i>Myoxocephalus scorpius</i>
moustache sculpin	<i>Triglops murrayi</i>
ribbed sculpin	<i>Triglops pingelli</i>
fish doctor	<i>Gymnelus viridis</i>
pale eelpout	<i>Lycodes pallidus</i>
Arctic eelpout	<i>Lycodes reticulatus</i>
Brackish Fish:	
Arctic shanny	<i>Stichaeus punctatus</i>
slender eelblenny	<i>Lumpenus fabricii</i>
righteye flounder	<i>Pleuronectidae sp.</i>
Canadian plaice	<i>Hippoglossoides platessoides</i>
Capelin:	
Capelin	<i>Mallotus villosus</i>
Continued on Next Page	

Appendix D. Hudson Bay Fish Species

Table D.1 Continued

Common Name	Species Name
Sandlance:	
northern sand lance	<i>Ammodytes dubius</i>
stout sand lance	<i>Ammodytes hexapterus</i>
Sharks/Rays:	
sleepers sharks	<i>Somniosidae</i>
skates	<i>Rajidae</i>
Other Marine Fish:	
alligator poacher	<i>Leptagonus decagonus</i>
Atlantic alligatorfish	<i>Ulcina olriki</i>
lumpfish	<i>Cyclopterus lumpus</i>
leatherfin lumpsucker	<i>Eumicrotremus derjugini</i>
Atlantic spiny lumpsucker	<i>Eumicrotremus spinosus</i>
sea tadpole	<i>Careproctus reinhardti</i>
gelatinous snailfish	<i>Liparis fabricii</i>
dusky snailfish	<i>Liparis gibbus</i>
kelp snailfish	<i>Liparis tunicatus</i>
stout eelblenny	<i>Anisarchus medius</i>
fourline snakeblenny	<i>Eumesogrammus praecisus</i>
daubed shanny	<i>Leptoclinus maculatus</i>
banded gunnel	<i>Pholis fasciata</i>
Atlantic Herring	<i>Clupea harengus</i>

Appendix E

Hudson Bay Model Vulnerabilities

Table E.1: Vulnerabilities used in the fitting of the Hudson Bay model

	Prey/predator	1	2	3	4	5	6	7	8	9	10	11	12
1	Polar Bear WHB	2											
2	SH Polar Bear		3										
3	Polar Bear Foxe			2									
4	Killer Whale												
5	Narwhal				10								
6	Bowhead				10								
7	Walrus N	2			10								
8	Walrus S		3		10								
9	Bearded Seal	2	3	2	10				2				
10	Harbour Seal	2	3	2	10								
11	Ringed Seal	2	3	2	10				10				
12	Harp seal	2	3	2	10								
13	Beluga E		3		2								
14	Beluga W	2		2	2								
15	Beluga James		10		2								
16	Seabirds	2	3	2	10								
17	Arctic Char					1				1			
18	Atlantic Salmon				10	1				1			1
19	Gadiformes				10	1		10	2	2	10	10	2
20	Sculpins/Zoarcids				10	1		2	2	1	10	10	1
21	Capelin					1				10	2	1	1
22	Sandlance									10	2	1	
23	Sharks/Rays				2								
24	Other Marine Fish			2	10	1		10	10	1	2	2	1
25	Brackish Fish			2		1				1	2		
26	Cephalopods			2	10	1				1	2	2	
27	MacroZooplankton			2		1	2			1	2	2	
28	Euphausiids			2		1	2				2	2	
29	Copepods			2			2						
30	Crustaceans			2		1	2	10	10	1	2	2	1
31	Other MesoZooplankton			2			2						
32	MicroZooplankton			2			2						
33	Marine Worms			2			2	10	10	10	10		
34	Echinoderms	10	10	2			2	10	10	10	10		
35	Bivalves	10	10	2			2	10	10				
36	Other Benthos	10	2	2			10	10	10	10	10		
37	Primary Production	2	2	2									
38	Ice Algae			2									
39	Ice Detritus			2									
40	Pelagic Detritus		2	2									

Table Continued on Next Page

Appendix E. Hudson Bay Model Vulnerabilities

Table E.1 Continued

	Prey/Predator	13	14	15	16	17	18	19	20	21	22	23	24
1	Polar Bear WHB												
2	SH Polar Bear												
3	Polar Bear Foxe												
4	Killer Whale												
5	Narwhal											2	
6	Bowhead												
7	Walrus N												
8	Walrus S												
9	Bearded Seal											2	
10	Harbour Seal												
11	Ringed Seal											2	
12	Harp seal											2	
13	Beluga E												
14	Beluga W												
15	Beluga James												
16	Seabirds				2								
17	Arctic Char		2		2		1					2	
18	Atlantic Salmon	2	2	2	2	1	1					2	
19	Gadiformes	1	10	2	2	2	10	2				1	
20	Sculpins/ Zoarcids	1	2		2	2	10		2			1	
21	Capelin	2	2	1	2	1	1	10	10			10	1
22	Sandlance		2		2	1	1	10	10			10	
23	Sharks/Rays											2	
24	Other Marine Fish		2		2	1	1	10	10			2	
25	Brackish Fish	2	2		2	1	1					2	
26	Cephalopods	2	2	1	2		1				1	2	1
27	MacroZooplankton		2		2	1	1			1	1	2	1
28	Euphausiids	2	2	2	2	1	1			2	2	2	1
29	Copepods	2	2	2	2	1	1			2	2		1
30	Crustaceans	2	2	2		1	1	2	2	2	2	2	1
31	Other MesoZooplankton				2	1	1			2	2		1
32	MicroZooplankton					1	1			2	2		1
33	Marine Worms	10	10	10	10	10		10	10			10	10
34	Echinoderms				10	10		10	10			10	
35	Bivalves				10			10	10			10	10
36	Other Benthos	10	10	10	10	10		10	10			10	10
37	Primary Production					1	1			1	1		1
38	Ice Algae					1	1	2	2				1
39	Ice Detritus							2	2				
40	Pelagic Detritus				1					1	1		1

Table Continued on Next Page

Appendix E. Hudson Bay Model Vulnerabilities

Table E.1 Continued

	Prey/Predator	25	26	27	28	29	30	31	32	33	34	35	36
1	Polar Bear WHB												
2	SH Polar Bear												
3	Polar Bear Foxe												
4	Killer Whale												
5	Narwhal												
6	Bowhead												
7	Walrus N												
8	Walrus S												
9	Bearded Seal												
10	Harbour Seal												
11	Ringed Seal												
12	Harp seal												
13	Beluga E												
14	Beluga W												
15	Beluga James												
16	Seabirds												
17	Arctic Char		2										
18	Atlantic Salmon		2										
19	Gadiformes		10										
20	Sculpins/Zoarcids		10										
21	Capelin	2	1										
22	Sandlance	2	1										
23	Sharks/Rays												
24	Other Marine Fish		2										
25	Brackish Fish	1											
26	Cephalopods	1	2										
27	MacroZooplankton	1	1		1					1			1
28	Euphausiids	1	1	2	1		2	1		2	2		
29	Copepods	1	1	2	1		1	1		1	2	1	
30	Crustaceans	1	1	2	1		1	2		2	2		
31	Other MesoZoopl.	1	1	2	1		2	1		1	2	1	1
32	MicroZoopl.	1	1	2	1	2	2	1		1	2	1	1
33	Marine Worms	10					10			10	10		10
34	Echinoderms	10					10			10	10		10
35	Bivalves						10				10		10
36	Other Benthos	10					10			10	10		10
37	Primary Production	1		1	1	1	1	1	1	1	1	1	1
38	Ice Algae	1		1	1	1	1	1	1	10	10	10	10
39	Ice Detritus						2			2	2	2	2
40	Pelagic Detritus	1		1	1	1	1	1	1				

Appendix F

Hudson Bay Mixed Trophic Impacts

Appendix F. Hudson Bay Mixed Trophic Impacts

Table F.1: Mixed Trophic Impact results from balanced Hudson Bay model by species groups. Harvest or fisheries are indicated by H preceding the species group or fishery

Impacting / Impacted	Polar Bear WHB	SH Polar Bear	Polar Bear Foxe	Killer Whale	Narwhal	Bowhead	Walrus N
1 Polar Bear WHB	-0.5300	-0.0237	-0.0328	-0.0255	0.0138	0.0035	-0.0133
2 SH Polar Bear	-0.0123	-0.5200	-0.0152	-0.0170	0.0050	0.0024	0.0007
3 Polar Bear Foxe	-0.0138	-0.0111	-0.5150	-0.0123	0.0057	0.0017	0.0004
4 Killer Whale	0.0047	0.0052	0.0036	-0.5080	-0.0630	-0.0726	-0.0109
5 Narwhal	-0.0006	-0.0005	-0.0007	0.0210	-0.4420	-0.0031	-0.0002
6 Bowhead	0.0000	0.0000	0.0000	0.0070	-0.0010	-0.4270	-0.0002
7 Walrus N	0.0012	-0.0002	-0.0003	0.0073	-0.0021	-0.0012	-0.4770
8 Walrus S	-0.0593	-0.0585	-0.0543	-0.0119	0.0179	0.0009	0.0004
9 Bearded Seal	0.0417	0.0420	0.0752	0.0464	-0.0057	-0.0070	-0.0021
10 Harbour Seal	-0.0007	-0.0007	0.0037	0.0063	-0.0022	-0.0009	-0.0001
11 Ringed Seal	0.1940	0.1970	0.1720	0.0670	-0.0671	-0.0070	-0.0035
12 Harp seal	0.0113	0.0112	0.0157	0.0114	-0.0018	-0.0016	-0.0007
13 Beluga E	-0.0003	0.0010	-0.0004	0.0021	-0.0016	-0.0004	0.0001
14 Beluga W	0.0282	-0.0095	0.0194	0.0481	-0.0267	-0.0073	-0.0008
15 Beluga James	-0.0013	0.0255	-0.0015	0.0189	-0.0033	-0.0028	-0.0004
16 Seabirds	-0.0019	0.0102	-0.0025	-0.0018	-0.0149	0.0007	-0.0044
17 Arctic Char	-0.0009	-0.0024	-0.0004	0.0008	-0.0018	-0.0006	-0.0001
18 Atlantic Salmon	-0.0058	-0.0060	-0.0057	-0.0039	-0.0167	0.0003	0.0024
19 Gadiformes	0.0220	0.0181	0.0237	0.0325	0.0955	-0.0038	-0.0130
20 Sculpins/ Zoarcids	0.0068	0.0059	0.0061	0.0125	0.0574	-0.0012	-0.0089
21 Capelin	0.0566	0.0644	0.0603	0.0523	0.0412	-0.0131	0.0002
22 Sandlance	0.0601	0.0606	0.0555	0.0243	-0.0197	-0.0101	-0.0015
23 Sharks/Rays	0.0000	0.0000	0.0000	0.0023	-0.0008	-0.0003	-0.0001
24 Other Marine Fish	0.0147	0.0132	0.0146	0.0165	0.0490	-0.0037	0.0149
25 Brackish Fish	0.0002	-0.0002	0.0007	0.0024	0.0058	-0.0002	0.0000
26 Cephalopods	-0.0129	-0.0122	-0.0135	-0.0046	0.0182	0.0024	0.0036
27 MacroZoopl.	0.0044	0.0058	0.0042	0.0043	0.0235	-0.0113	0.0035
28 Euphausiids	0.0178	0.0185	0.0169	0.0182	0.0220	0.0720	0.0030
29 Copepods	0.0125	0.0133	0.0117	0.0118	-0.0064	0.1960	-0.0045
30 Crustaceans	0.0281	0.0282	0.0346	0.0269	0.0683	-0.0015	-0.0746
31 Other Meso-Zoopl.	-0.0128	-0.0126	-0.0138	-0.0135	-0.0239	-0.0624	0.0227
32 MicroZoopl.	0.0017	0.0029	0.0018	0.0009	-0.0014	-0.0023	0.0113
33 Marine Worms	-0.0124	-0.0063	-0.0046	0.0036	0.0081	-0.0028	0.0247
34 Echinoderms	0.0012	0.0060	0.0067	0.0032	0.0047	-0.0027	0.0779
35 Bivalves	-0.0140	-0.0070	-0.0081	0.0027	0.0230	0.0072	0.1540
36 Other Benthos	0.0354	0.0130	0.0135	0.0110	0.0121	0.0212	-0.0155
37 Primary Production	0.0325	0.0351	0.0331	0.0274	0.0233	0.1130	0.0062
38 Ice Algae	0.0151	0.0121	0.0131	0.0149	0.0329	0.0335	0.0183
39 Ice Detritus	0.0109	0.0064	0.0082	0.0179	0.0474	0.0158	0.1360
40 Pelagic Detritus	0.0094	0.0106	0.0100	0.0082	0.0117	0.0075	-0.0046
41 H: SH Polar Bear	0.0090	-0.3520	0.0111	0.0125	-0.0037	-0.0018	-0.0005
42 H: WHB Polar Bear	-0.2870	0.0145	0.0200	0.0155	-0.0084	-0.0022	0.0081
43 H: FB Polar Bear	0.0099	0.0079	-0.3470	0.0088	-0.0041	-0.0012	-0.0003
44 H: Killer whale	-0.0047	-0.0052	-0.0036	-0.4920	0.0630	0.0726	0.0109
45 H: Bowhead	0.0000	0.0000	0.0000	-0.0052	0.0007	-0.4250	0.0001
46 H: Narwhal	0.0005	0.0004	0.0005	-0.0162	-0.4310	0.0024	0.0001
47 H: N Walrus	-0.0011	0.0001	0.0002	-0.0066	0.0019	0.0010	-0.4730
48 H: S Walrus	0.0259	0.0256	0.0237	0.0052	-0.0078	-0.0004	-0.0002
49 H: Beluga E	0.0003	-0.0009	0.0003	-0.0018	0.0014	0.0003	-0.0001
50 H: Beluga W	-0.0082	0.0028	-0.0057	-0.0140	0.0078	0.0021	0.0002
51 H: Beluga S	0.0002	-0.0049	0.0003	-0.0037	0.0006	0.0005	0.0001
52 H: Sealing	-0.0401	-0.0406	-0.0497	-0.0268	0.0112	0.0036	0.0013
53 H: Bird Hunting	0.0000	-0.0002	0.0000	0.0000	0.0002	0.0000	0.0001
54 H: Fishing	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000

Table Continued on Next Page

Appendix F. Hudson Bay Mixed Trophic Impacts

Table F.1 Continued

Impacting / Impacted	Walrus S	Bearded Seal	Harbour Seal	Ringed Seal	Harp seal	Beluga E	Beluga W
1 Polar Bear WHB	0.0095	-0.0635	0.0009	-0.0607	-0.1130	0.0065	-0.1500
2 SH Polar Bear	-0.0940	-0.0648	-0.0163	-0.0228	-0.1110	-0.0252	0.0103
3 Polar Bear Foxe	0.0045	-0.0528	-0.1840	-0.0226	-0.0682	0.0027	-0.0474
4 Killer Whale	-0.0937	-0.0161	-0.1030	0.0260	-0.0261	-0.0089	-0.0381
5 Narwhal	-0.0043	-0.0031	-0.0053	-0.0007	-0.0007	-0.0020	-0.0038
6 Bowhead	-0.0013	-0.0003	-0.0016	0.0002	-0.0006	-0.0003	-0.0007
7 Walrus N	-0.0037	-0.0017	-0.0023	0.0002	-0.0001	-0.0004	-0.0015
8 Walrus S	-0.2940	0.0513	0.0931	-0.2120	0.0890	0.0104	0.0409
9 Bearded Seal	-0.0177	-0.1050	-0.0922	-0.0385	-0.0765	-0.0030	-0.0274
10 Harbour Seal	-0.0013	-0.0025	-0.0057	-0.0030	-0.0034	-0.0007	-0.0019
11 Ringed Seal	-0.0410	-0.3140	-0.3090	-0.2760	-0.2910	-0.0363	-0.1380
12 Harp seal	-0.0046	-0.0137	-0.0158	-0.0068	-0.0252	-0.0013	-0.0084
13 Beluga E	-0.0006	-0.0011	-0.0009	-0.0006	-0.0013	-0.4640	-0.0010
14 Beluga W	-0.0107	-0.0342	-0.0306	-0.0172	-0.0537	-0.0102	-0.2710
15 Beluga James	-0.0088	-0.0053	-0.0062	-0.0018	-0.0164	-0.0025	-0.0026
16 Seabirds	-0.0073	-0.0170	-0.0259	-0.0108	-0.0496	-0.0101	-0.0271
17 Arctic Char	-0.0012	0.0195	-0.0138	-0.0115	-0.0123	-0.0036	0.0307
18 Atlantic Salmon	0.0019	0.0000	-0.0221	-0.0174	-0.0092	-0.0008	-0.0072
19 Gadiformes	0.0138	0.0979	-0.0229	0.0482	-0.1010	0.0284	0.0634
20 Sculpins/ Zoar-	-0.0153	-0.0002	0.0074	0.0268	-0.0664	0.0413	-0.0037
cids							
21 Capelin	-0.0188	0.0609	0.0854	0.1170	0.7100	0.0377	0.0971
22 Sandlance	-0.0122	-0.0557	0.0973	0.2150	-0.1080	-0.0132	-0.0388
23 Sharks/Rays	-0.0004	-0.0001	-0.0005	0.0001	-0.0005	0.0000	-0.0002
24 Other Marine	0.0292	0.0147	0.0620	0.0408	-0.0116	-0.0061	0.0136
Fish							
25 Brackish Fish	-0.0008	0.0135	0.0497	-0.0069	-0.0142	0.0081	0.0245
26 Cephalopods	0.0016	-0.0191	-0.0116	-0.0382	-0.0497	0.0087	0.0102
27 MacroZoopl.	0.0005	0.0005	0.0151	0.0072	0.0413	-0.0150	0.0009
28 Euphausiids	-0.0028	0.0022	0.0299	0.0390	0.0836	0.0657	0.0650
29 Copepods	-0.0110	-0.0237	0.0114	0.0405	0.0325	0.0422	0.0403
30 Crustaceans	-0.0722	0.1450	0.0441	0.0765	0.0502	0.0572	0.0395
31 Other Meso-	0.0259	-0.0348	-0.0175	-0.0307	-0.0434	-0.0464	-0.0391
Zoopl.							
32 MicroZoopl.	0.0094	-0.0120	0.0129	0.0063	0.0155	-0.0108	-0.0019
33 Marine Worms	0.0427	0.0080	0.0173	-0.0092	-0.0112	0.0158	0.0179
34 Echinoderms	0.0336	0.0618	0.0111	-0.0149	-0.0204	-0.0149	-0.0116
35 Bivalves	0.2130	0.0224	0.0208	-0.0548	0.0218	0.0018	0.0096
36 Other Benthos	-0.0280	0.0363	0.0176	0.0089	-0.0418	0.0752	0.0566
37 Primary Produc-	-0.0001	0.0147	0.0649	0.0873	0.1420	0.0326	0.0497
tion							
38 Ice Algae	0.0236	0.0378	0.0253	0.0218	-0.0064	0.0317	0.0336
39 Ice Detritus	0.1620	0.0882	0.0455	-0.0320	-0.0332	0.0654	0.0564
40 Pelagic Detritus	-0.0055	0.0129	0.0198	0.0248	0.0394	0.0075	0.0110
41 H: SH Polar Bear	0.0690	0.0475	0.0119	0.0167	0.0816	0.0185	-0.0075
42 H: WHB Polar Bear	-0.0058	0.0387	-0.0005	0.0371	0.0690	-0.0040	0.0918
43 H: FB Polar Bear	-0.0032	0.0377	0.1310	0.0162	0.0487	-0.0019	0.0338
44 H: Killer whale	0.0937	0.0161	0.1030	-0.0260	0.0261	0.0089	0.0381
45 H: Bowhead	0.0010	0.0002	0.0012	-0.0002	0.0004	0.0002	0.0005
46 H: Narwhal	0.0034	0.0024	0.0041	0.0006	0.0005	0.0015	0.0029
47 H: N Walrus	0.0033	0.0016	0.0021	-0.0002	0.0001	0.0004	0.0013
48 H: S Walrus	-0.3080	-0.0224	-0.0407	0.0926	-0.0389	-0.0045	-0.0179
49 H: Beluga E	0.0005	0.0010	0.0007	0.0005	0.0011	-0.4620	0.0008
50 H: Beluga W	0.0031	0.0099	0.0089	0.0050	0.0156	0.0030	-0.2120
51 H: Beluga S	0.0017	0.0010	0.0012	0.0003	0.0032	0.0005	0.0005
52 H: Sealing	0.0120	-0.2470	-0.1350	-0.0788	-0.0951	0.0060	0.0284
53 H: Bird Hunting	0.0001	0.0003	0.0004	0.0002	0.0008	0.0002	0.0004
54 H: Fishing	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000

Table Continued on Next Page

Appendix F. Hudson Bay Mixed Trophic Impacts

Table F.1 Continued

Impacting / Impacted	Beluga James	Seabirds	Arctic Char	Atlantic Salmon	Gadiformes	Sculpins/ Zoarcids	Capelin
1 Polar Bear WHB	0.0273	0.0038	0.0405	0.0142	0.0451	0.0226	0.0210
2 SH Polar Bear	-0.2840	0.0003	-0.0019	0.0018	0.0106	0.0079	0.0090
3 Polar Bear Foxe	0.0120	0.0015	0.0133	0.0050	0.0173	0.0096	0.0085
4 Killer Whale	-0.0383	0.0003	0.0106	0.0041	-0.0007	-0.0047	0.0008
5 Narwhal	-0.0022	-0.0008	-0.0010	-0.0026	-0.0148	-0.0130	0.0001
6 Bowhead	-0.0008	-0.0001	0.0002	-0.0001	0.0000	0.0000	-0.0003
7 Walrus N	-0.0002	-0.0004	0.0005	0.0000	-0.0045	-0.0034	0.0010
8 Walrus S	0.0481	0.0041	-0.0130	-0.0042	0.0664	0.0629	0.0230
9 Bearded Seal	-0.0278	0.0003	-0.0111	-0.0087	-0.0032	0.0063	0.0028
10 Harbour Seal	-0.0014	-0.0008	0.0007	0.0002	-0.0037	-0.0050	-0.0029
11 Ringed Seal	-0.1640	-0.0142	0.0469	0.0156	-0.2400	-0.2170	-0.0757
12 Harp seal	-0.0135	-0.0008	0.0033	-0.0030	0.0029	0.0016	-0.0145
13 Beluga E	-0.0017	-0.0004	0.0016	-0.0062	-0.0033	-0.0075	-0.0013
14 Beluga W	-0.0250	-0.0107	-0.1910	-0.0609	-0.0933	-0.0091	-0.0491
15 Beluga James	-0.1840	-0.0008	0.0019	-0.0019	-0.0011	0.0012	-0.0114
16 Seabirds	-0.0331	-0.5210	-0.1520	-0.1660	0.0036	-0.0152	-0.0533
17 Arctic Char	-0.0045	0.0083	-0.0100	-0.0801	-0.0156	-0.0190	-0.0118
18 Atlantic Salmon	-0.0106	-0.0077	-0.0948	-0.1120	-0.0163	-0.0314	-0.0350
19 Gadiformes	-0.0131	-0.0061	-0.0245	-0.0002	-0.1410	-0.0629	-0.0903
20 Sculpins/ Zoar-	-0.0345	0.0044	-0.0049	0.0037	-0.0438	-0.1140	-0.0689
cids							
21 Capelin	0.3330	0.0555	-0.0491	-0.0250	-0.0247	-0.0115	-0.0906
22 Sandlance	-0.0639	0.0073	0.0301	0.0131	-0.0206	-0.0092	-0.0419
23 Sharks/Rays	-0.0002	0.0000	0.0001	0.0000	0.0000	0.0000	0.0000
24 Other Marine	-0.0330	0.0127	0.0073	0.0019	0.0364	0.0211	-0.0483
Fish							
25 Brackish Fish	-0.0084	0.0439	-0.0041	0.0047	-0.0011	0.0007	-0.0157
26 Cephalopods	0.0117	0.0305	-0.1400	-0.1010	-0.0988	-0.1610	-0.0718
27 MacroZoopl.	0.0035	0.0658	0.0123	0.0489	-0.0103	-0.0262	0.0551
28 Euphausiids	0.1010	0.0299	-0.0719	0.0614	-0.0038	-0.0012	0.1200
29 Copepods	0.0589	-0.0014	0.1130	-0.0582	-0.0336	-0.0207	0.0579
30 Crustaceans	0.0565	-0.0063	0.0417	0.1380	-0.1370	-0.0784	0.0517
31 Other Meso-	-0.0581	-0.0010	0.0552	-0.0626	0.0283	0.0091	-0.0556
Zoopl.							
32 MicroZoopl.	-0.0020	0.0196	0.0265	0.0872	-0.0123	-0.0230	0.0246
33 Marine Worms	0.0084	-0.0030	0.0059	-0.0119	0.0650	0.0619	-0.0221
34 Echinoderms	-0.0245	0.0044	0.0143	-0.0122	0.0832	0.0449	-0.0129
35 Bivalves	0.0042	0.0390	-0.0390	0.0017	0.0762	0.0648	0.0045
36 Other Benthos	0.0481	-0.0024	0.0019	-0.0118	0.0637	0.0701	-0.0286
37 Primary Produc-	0.0872	0.0463	0.1560	0.1140	-0.0558	-0.0499	0.2000
tion							
38 Ice Algae	0.0194	0.0165	0.0444	0.0437	0.0974	0.0602	-0.0013
39 Ice Detritus	0.0314	0.0253	-0.0139	-0.0047	0.1850	0.2260	-0.0399
40 Pelagic Detritus	0.0201	0.0353	0.0036	0.0109	-0.0148	-0.0117	0.0522
41 H: SH Polar Bear	0.2080	-0.0002	0.0014	-0.0013	-0.0077	-0.0058	-0.0066
42 H: WHB Polar	-0.0167	-0.0023	-0.0247	-0.0086	-0.0275	-0.0138	-0.0128
Bear							
43 H: FB Polar Bear	-0.0086	-0.0011	-0.0095	-0.0036	-0.0123	-0.0068	-0.0061
44 H: Killer whale	0.0383	-0.0003	-0.0106	-0.0041	0.0007	0.0047	-0.0008
45 H: Bowhead	0.0006	0.0001	-0.0001	0.0001	0.0000	0.0000	0.0002
46 H: Narwhal	0.0017	0.0006	0.0008	0.0020	0.0114	0.0101	-0.0001
47 H: N Walrus	0.0002	0.0004	-0.0005	0.0000	0.0040	0.0031	-0.0009
48 H: S Walrus	-0.0210	-0.0018	0.0057	0.0018	-0.0290	-0.0275	-0.0100
49 H: Beluga E	0.0015	0.0003	-0.0014	0.0053	0.0028	0.0065	0.0011
50 H: Beluga W	0.0073	0.0031	0.0556	0.0177	0.0271	0.0027	0.0143
51 H: Beluga S	-0.1580	0.0002	-0.0004	0.0004	0.0002	-0.0002	0.0022
52 H: Sealing	0.0325	0.0020	-0.0031	0.0013	0.0322	0.0266	0.0118
53 H: Bird Hunting	0.0005	-0.0079	0.0025	0.0027	-0.0001	0.0003	0.0009
54 H: Fishing	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000

Table Continued on Next Page

Appendix F. Hudson Bay Mixed Trophic Impacts

Table F.1 Continued

Impacting/Impacted	Sandlance	Shark/Ray	Other Marine Fish	Brackish Fish	Cephalopods	Macro-Zoopl.	Euphsids
1 Polar Bear WHB	0.0162	0.0348	0.0013	0.0076	0.0118	-0.0070	-0.0001
2 SH Polar Bear	0.0077	0.0169	0.0011	-0.0008	0.0020	-0.0019	-0.0005
3 Polar Bear Foxe	0.0072	0.0152	0.0012	0.0036	0.0041	-0.0027	-0.0002
4 Killer Whale	-0.0105	-0.4420	-0.0006	0.0034	0.0024	-0.0004	0.0010
5 Narwhal	0.0052	-0.0176	-0.0017	-0.0021	-0.0094	0.0001	-0.0003
6 Bowhead	-0.0003	-0.0064	-0.0001	-0.0001	0.0000	-0.0006	-0.0016
7 Walrus N	0.0010	-0.0084	-0.0047	0.0003	0.0000	-0.0003	-0.0004
8 Walrus S	0.0755	0.0338	0.0067	-0.0056	0.0075	-0.0061	-0.0042
9 Bearded Seal	0.0143	-0.0331	0.0033	-0.0002	0.0025	-0.0006	-0.0002
10 Harbour Seal	-0.0045	-0.0078	-0.0034	-0.0064	-0.0006	0.0008	0.0003
11 Ringed Seal	-0.2550	-0.1430	-0.0305	0.0195	-0.0259	0.0200	0.0136
12 Harp seal	0.0027	-0.0007	-0.0013	0.0021	0.0010	0.0024	0.0004
13 Beluga E	0.0022	-0.0034	0.0026	-0.0016	-0.0033	0.0008	-0.0006
14 Beluga W	0.0293	-0.0706	0.0080	-0.0408	-0.0419	0.0203	-0.0055
15 Beluga James	0.0014	-0.0175	0.0009	0.0011	-0.0029	0.0022	0.0000
16 Seabirds	0.0004	-0.0299	-0.0327	-0.2360	-0.1140	0.0152	-0.0017
17 Arctic Char	-0.0112	0.0341	-0.0256	-0.0647	0.0129	-0.0183	0.0036
18 Atlantic Salmon	0.0024	-0.0081	-0.0387	-0.1540	-0.1280	-0.0393	0.0032
19 Gadiformes	-0.1380	0.0508	-0.2560	-0.0014	0.0455	0.0292	0.0061
20 Sculpins/ Zoarcids	-0.1060	0.0882	-0.1310	-0.0045	0.0431	0.0189	0.0056
21 Capelin	-0.0592	-0.0161	-0.0219	-0.0474	0.0177	-0.1460	-0.0277
22 Sandlance	-0.0898	0.0350	-0.0399	0.0006	-0.0891	-0.0386	-0.0346
23 Sharks/Rays	-0.0001	-0.0495	0.0000	0.0000	0.0000	0.0000	0.0000
24 Other Marine Fish	-0.0245	0.0417	-0.0374	-0.0205	-0.0359	-0.0149	0.0051
25 Brackish Fish	-0.0060	0.0295	-0.0072	-0.0487	-0.0357	-0.0193	0.0039
26 Cephalopods	-0.0645	-0.0059	0.0435	0.0158	-0.1090	-0.0600	0.0206
27 MacroZoopl.	-0.0313	0.0450	0.0223	0.0648	0.0915	-0.0561	-0.1970
28 Euphausiids	0.0390	-0.0014	-0.0224	0.0445	-0.0190	-0.0601	-0.1080
29 Copepods	0.1340	-0.0102	0.0303	-0.1160	-0.0116	-0.1470	0.3320
30 Crustaceans	0.0109	-0.0327	0.1770	0.0907	0.0509	0.0256	-0.0682
31 Other Meso-Zoopl.	0.0095	0.0131	-0.0423	-0.0191	0.0513	0.0154	-0.3700
32 MicroZoopl.	0.0545	0.0183	-0.0271	0.1260	0.0719	0.1600	-0.0289
33 Marine Worms	-0.0180	0.0417	0.0041	-0.0126	-0.0054	-0.0413	-0.0104
34 Echinoderms	-0.0118	0.0944	-0.0644	0.0063	0.0110	0.0338	-0.0276
35 Bivalves	-0.0040	0.0125	0.0090	-0.0238	-0.0118	0.0267	0.0689
36 Other Benthos	-0.0164	0.0049	-0.0110	0.0296	-0.0114	-0.1490	0.0276
37 Primary Production	0.2180	0.0265	0.1190	0.1160	0.0789	0.1910	0.1110
38 Ice Algae	0.0100	0.0332	0.0772	0.0237	0.0335	0.0690	0.0318
39 Ice Detritus	-0.0444	0.0836	-0.0305	0.0063	-0.0034	-0.0852	0.0428
40 Pelagic Detritus	0.0350	0.0037	0.0783	0.0494	0.0049	0.0439	0.0128
41 H: SH Polar Bear	-0.0056	-0.0124	-0.0008	0.0006	-0.0015	0.0014	0.0004
42 H: WHB Polar Bear	-0.0099	-0.0212	-0.0008	-0.0047	-0.0072	0.0043	0.0001
43 H: FB Polar Bear	-0.0052	-0.0109	-0.0008	-0.0026	-0.0029	0.0019	0.0001
44 H: Killer whale	0.0105	0.4420	0.0006	-0.0034	-0.0024	0.0004	-0.0010
45 H: Bowhead	0.0002	0.0047	0.0001	0.0001	0.0000	0.0005	0.0012
46 H: Narwhal	-0.0040	0.0136	0.0013	0.0016	0.0073	-0.0001	0.0002
47 H: N Walrus	-0.0009	0.0076	0.0043	-0.0002	0.0000	0.0003	0.0004
48 H: S Walrus	-0.0330	-0.0148	-0.0029	0.0024	-0.0033	0.0027	0.0018
49 H: Beluga E	-0.0019	0.0029	-0.0023	0.0014	0.0029	-0.0007	0.0005
50 H: Beluga W	-0.0085	0.0205	-0.0023	0.0119	0.0122	-0.0059	0.0016
51 H: Beluga S	-0.0003	0.0034	-0.0002	-0.0002	0.0006	-0.0004	0.0000
52 H: Sealing	0.0286	0.0308	0.0038	-0.0014	0.0025	-0.0029	-0.0018
53 H: Bird Hunting	0.0000	0.0005	0.0005	0.0039	0.0019	-0.0003	0.0000
54 H: Fishing	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000

Table Continued on Next Page

Appendix F. Hudson Bay Mixed Trophic Impacts

Table F.1 Continued

Impacting/Impacted	Copepods	Crustaceans	Other Meso- Zoopl.	Micro- Zoopl.	Marine Worms	Echino- derms	Bivalves
1 Polar Bear WHB	0.0001	-0.0006	0.0004	0.0009	-0.0015	-0.0047	-0.0021
2 SH Polar Bear	0.0001	-0.0001	0.0001	0.0002	-0.0005	-0.0009	-0.0003
3 Polar Bear Foxe	0.0001	-0.0002	0.0002	0.0003	-0.0006	-0.0018	-0.0009
4 Killer Whale	-0.0002	0.0003	0.0000	0.0001	0.0003	0.0004	0.0005
5 Narwhal	0.0001	-0.0003	-0.0003	-0.0001	0.0009	0.0020	0.0010
6 Bowhead	0.0003	-0.0003	0.0003	0.0000	-0.0001	0.0000	0.0001
7 Walrus N	0.0002	-0.0007	0.0013	0.0000	0.0011	-0.0057	-0.0051
8 Walrus S	0.0007	-0.0021	0.0006	0.0005	-0.0038	-0.0091	-0.0059
9 Bearded Seal	0.0000	-0.0021	-0.0004	0.0001	0.0005	-0.0005	0.0007
10 Harbour Seal	-0.0001	0.0002	-0.0001	-0.0001	0.0002	0.0003	0.0004
11 Ringed Seal	-0.0023	0.0065	-0.0005	-0.0016	0.0139	0.0286	0.0137
12 Harp seal	-0.0003	0.0008	-0.0002	-0.0002	-0.0002	-0.0006	-0.0003
13 Beluga E	0.0001	-0.0007	-0.0002	-0.0002	-0.0001	0.0010	0.0005
14 Beluga W	0.0008	0.0003	-0.0013	-0.0032	0.0002	0.0098	0.0039
15 Beluga James	-0.0001	0.0001	-0.0001	-0.0002	-0.0003	0.0001	0.0001
16 Seabirds	-0.0001	0.0183	0.0051	-0.0014	-0.0007	-0.0114	-0.0135
17 Arctic Char	-0.0023	-0.0042	-0.0045	0.0049	-0.0015	0.0001	0.0035
18 Atlantic Salmon	0.0027	-0.0253	0.0034	0.0022	0.0067	0.0146	0.0067
19 Gadiformes	-0.0007	0.0111	0.0094	-0.0028	-0.0238	-0.0756	-0.0248
20 Sculpins/ Zoar- cids	-0.0003	-0.0077	0.0082	-0.0016	-0.0202	-0.0349	-0.0216
21 Capelin	0.0155	-0.0388	0.0101	0.0109	0.0067	0.0192	0.0084
22 Sandlance	0.0033	-0.0133	-0.0172	0.0028	0.0034	0.0075	0.0035
23 Sharks/Rays	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
24 Other Marine Fish	-0.0026	-0.0509	0.0038	0.0043	-0.0068	0.0191	-0.0050
25 Brackish Fish	0.0006	-0.0070	0.0012	0.0015	0.0004	0.0008	0.0015
26 Cephalopods	-0.0021	-0.0033	-0.0040	0.0100	0.0079	0.0183	0.0075
27 MacroZoopl.	0.0077	-0.0666	-0.1200	-0.1430	0.0172	0.0235	0.0019
28 Euphausiids	-0.3220	0.0037	-0.0605	0.1970	0.0104	0.0149	0.0024
29 Copepods	-0.3750	-0.0674	-0.1680	-0.4600	0.0016	0.0178	-0.0092
30 Crustaceans	-0.0194	-0.0531	0.0397	-0.0051	-0.1660	-0.3930	-0.1660
31 Other Meso- Zoopl.	0.0093	-0.2240	-0.0614	-0.1510	0.0389	0.0890	0.0684
32 MicroZoopl.	-0.0932	-0.0910	-0.0557	-0.1370	0.0204	0.0534	0.0353
33 Marine Worms	0.0004	-0.0321	-0.0303	0.0019	-0.0851	-0.0163	-0.0035
34 Echinoderms	0.0090	-0.0813	0.0519	-0.0098	-0.1710	0.0119	-0.1930
35 Bivalves	-0.0202	0.0605	-0.2050	0.0015	-0.1490	-0.0520	-0.1790
36 Other Benthos	-0.0038	0.0606	0.0298	0.0173	-0.1250	-0.1480	-0.2360
37 Primary Produc- tion	0.3210	0.0412	0.2310	0.2570	0.0085	0.0083	0.0270
38 Ice Algae	0.0802	0.0762	0.1370	0.0249	0.0343	0.0039	0.0190
39 Ice Detritus	-0.0147	0.1240	-0.1160	0.0088	0.2820	0.2250	0.3180
40 Pelagic Detritus	0.0105	0.0643	0.0302	0.0396	-0.0117	-0.0260	-0.0111
41 H: SH Polar Bear	-0.0001	0.0001	-0.0001	-0.0001	0.0004	0.0007	0.0002
42 H: WHB Polar Bear	0.0000	0.0003	-0.0002	-0.0006	0.0009	0.0029	0.0013
43 H: FB Polar Bear	0.0000	0.0002	-0.0001	-0.0002	0.0004	0.0013	0.0007
44 H: Killer whale	0.0002	-0.0003	0.0000	-0.0001	-0.0003	-0.0004	-0.0005
45 H: Bowhead	-0.0002	0.0002	-0.0002	0.0000	0.0001	0.0000	-0.0001
46 H: Narwhal	0.0000	0.0002	0.0002	0.0000	-0.0007	-0.0016	-0.0007
47 H: N Walrus	-0.0001	0.0006	-0.0012	0.0000	-0.0010	0.0051	0.0046
48 H: S Walrus	-0.0003	0.0009	-0.0003	-0.0002	0.0017	0.0040	0.0026
49 H: Beluga E	-0.0001	0.0006	0.0001	0.0001	0.0001	-0.0009	-0.0005
50 H: Beluga W	-0.0002	-0.0001	0.0004	0.0009	-0.0001	-0.0028	-0.0011
51 H: Beluga S	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
52 H: Sealing	0.0003	-0.0003	0.0003	0.0002	-0.0020	-0.0035	-0.0020
53 H: Bird Hunting	0.0000	-0.0003	-0.0001	0.0000	0.0000	0.0002	0.0002
54 H: Fishing	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000

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Appendix F. Hudson Bay Mixed Trophic Impacts

Table F.1 Continued

Impacting/Impacted	Other Benthos	Primary Production	Ice Algae	Ice Detritus	Pelagic Detritus	H: SH Polar Bear	H: WHB Polar Bear
1 Polar Bear WHB	0.0002	-0.0002	0.0000	0.0012	-0.0001	-0.0237	0.4700
2 SH Polar Bear	-0.0001	-0.0001	0.0000	0.0003	-0.0001	0.4800	-0.0123
3 Polar Bear Foxe	0.0001	-0.0001	0.0000	0.0005	-0.0001	-0.0111	-0.0138
4 Killer Whale	0.0000	0.0000	0.0000	-0.0003	0.0000	0.0052	0.0047
5 Narwhal	0.0001	0.0000	0.0000	-0.0006	0.0000	-0.0005	-0.0006
6 Bowhead	-0.0001	-0.0001	-0.0001	0.0000	0.0000	0.0000	0.0000
7 Walrus N	0.0009	-0.0001	0.0000	0.0016	-0.0001	-0.0002	0.0012
8 Walrus S	0.0000	-0.0004	0.0001	0.0032	-0.0002	-0.0585	-0.0593
9 Bearded Seal	0.0003	0.0000	0.0001	-0.0003	0.0002	0.0420	0.0417
10 Harbour Seal	0.0000	0.0000	0.0000	-0.0002	0.0000	-0.0007	-0.0007
11 Ringed Seal	0.0011	0.0012	-0.0003	-0.0091	0.0006	0.1970	0.1940
12 Harp seal	-0.0001	0.0002	0.0001	0.0001	0.0001	0.0112	0.0113
13 Beluga E	-0.0001	0.0000	0.0000	-0.0001	0.0001	0.0010	-0.0003
14 Beluga W	-0.0017	0.0002	0.0000	-0.0012	0.0002	-0.0095	0.0282
15 Beluga James	-0.0001	0.0001	0.0001	0.0001	0.0001	0.0255	-0.0013
16 Seabirds	-0.0021	-0.0004	-0.0004	0.0056	-0.0026	0.0102	-0.0019
17 Arctic Char	0.0005	0.0008	0.0012	-0.0009	0.0012	-0.0024	-0.0009
18 Atlantic Salmon	0.0033	-0.0014	-0.0011	-0.0046	0.0020	-0.0060	-0.0058
19 Gadiformes	-0.0042	0.0002	0.0002	0.0178	-0.0007	0.0181	0.0220
20 Sculpins/ Zoarcids	-0.0020	0.0002	0.0008	0.0131	0.0005	0.0059	0.0068
21 Capelin	0.0029	-0.0100	-0.0058	-0.0049	-0.0039	0.0644	0.0566
22 Sandlance	0.0020	-0.0006	0.0015	-0.0025	0.0013	0.0606	0.0601
23 Sharks/Rays	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
24 Other Marine Fish	0.0080	0.0014	0.0010	0.0011	0.0023	0.0132	0.0147
25 Brackish Fish	-0.0006	-0.0005	-0.0001	-0.0002	0.0000	-0.0002	0.0002
26 Cephalopods	0.0009	-0.0001	0.0004	-0.0050	0.0006	-0.0122	-0.0129
27 MacroZoopl.	0.0192	0.0287	0.0151	-0.0096	0.0233	0.0058	0.0044
28 Euphausiids	0.0176	0.1360	0.1120	-0.0101	0.0611	0.0185	0.0178
29 Copepods	-0.0331	-0.2480	-0.2130	0.0163	-0.1400	0.0133	0.0125
30 Crustaceans	-0.1270	-0.0114	-0.0070	0.1230	-0.0784	0.0282	0.0281
31 Other Meso-Zoopl.	0.0200	-0.0257	-0.0646	-0.0357	-0.0065	-0.0126	-0.0128
32 MicroZoopl.	-0.0080	-0.1570	-0.0898	-0.0131	-0.1930	0.0029	0.0017
33 Marine Worms	-0.3050	0.0023	0.0055	-0.0700	0.0070	-0.0063	-0.0124
34 Echinoderms	-0.0420	-0.0036	0.0045	0.0713	0.0017	0.0060	0.0012
35 Bivalves	-0.1090	0.0198	0.0043	-0.2260	0.0167	-0.0070	-0.0140
36 Other Benthos	-0.1430	-0.0073	-0.0593	-0.1910	-0.0063	0.0130	0.0354
37 Primary Production	-0.0259	-0.2800	-0.2300	-0.0039	-0.2550	0.0351	0.0325
38 Ice Algae	0.1150	-0.0690	-0.0740	-0.0575	-0.0661	0.0121	0.0151
39 Ice Detritus	0.2730	0.0079	-0.0316	0.0000	0.0047	0.0064	0.0109
40 Pelagic Detritus	-0.0117	-0.0209	-0.0167	0.0094	0.0000	0.0106	0.0094
41 H: SH Polar Bear	0.0001	0.0001	0.0000	-0.0002	0.0001	-0.3520	0.0090
42 H: WHB Polar Bear	-0.0001	0.0001	0.0000	-0.0007	0.0001	0.0145	-0.2870
43 H: FB Polar Bear	-0.0001	0.0001	0.0000	-0.0004	0.0000	0.0079	0.0099
44 H: Killer whale	0.0000	0.0000	0.0000	0.0003	0.0000	-0.0052	-0.0047
45 H: Bowhead	0.0001	0.0001	0.0001	0.0000	0.0000	0.0000	0.0000
46 H: Narwhal	-0.0001	0.0000	0.0000	0.0005	0.0000	0.0004	0.0005
47 H: N Walrus	-0.0008	0.0001	0.0000	-0.0014	0.0001	0.0001	-0.0011
48 H: S Walrus	0.0000	0.0002	0.0000	-0.0014	0.0001	0.0256	0.0259
49 H: Beluga E	0.0001	0.0000	0.0000	0.0001	0.0000	-0.0009	0.0003
50 H: Beluga W	0.0005	-0.0001	0.0000	0.0004	-0.0001	0.0028	-0.0082
51 H: Beluga S	0.0000	0.0000	0.0000	0.0000	0.0000	-0.0049	0.0002
52 H: Sealing	-0.0002	-0.0002	0.0000	0.0013	-0.0002	-0.0406	-0.0401
53 H: Bird Hunting	0.0000	0.0000	0.0000	-0.0001	0.0000	-0.0002	0.0000
54 H: Fishing	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000

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Appendix F. Hudson Bay Mixed Trophic Impacts

Table F.1 Continued							
Impacting/Impacted	H: FB Polar Bear	H: Killer whale	H: Bow- head	H: Nar- whal	H: N Walrus	H: S Walrus	
1 Polar Bear WHB	-0.0328	-0.0255	0.0035	0.0138	-0.0133	0.0095	
2 SH Polar Bear	-0.0152	-0.0170	0.0024	0.0050	0.0007	-0.0940	
3 Polar Bear Foxe	0.4850	-0.0123	0.0017	0.0057	0.0004	0.0045	
4 Killer Whale	0.0036	0.4920	-0.0726	-0.0630	-0.0109	-0.0937	
5 Narwhal	-0.0007	0.0210	-0.0031	0.5580	-0.0002	-0.0043	
6 Bowhead	0.0000	0.0070	0.5730	-0.0010	-0.0002	-0.0013	
7 Walrus N	-0.0003	0.0073	-0.0012	-0.0021	0.5230	-0.0037	
8 Walrus S	-0.0543	-0.0119	0.0009	0.0179	0.0004	0.7060	
9 Bearded Seal	0.0752	0.0464	-0.0070	-0.0057	-0.0021	-0.0177	
10 Harbour Seal	0.0037	0.0063	-0.0009	-0.0022	-0.0001	-0.0013	
11 Ringed Seal	0.1720	0.0670	-0.0070	-0.0671	-0.0035	-0.0410	
12 Harp seal	0.0157	0.0114	-0.0016	-0.0018	-0.0007	-0.0046	
13 Beluga E	-0.0004	0.0021	-0.0004	-0.0016	0.0001	-0.0006	
14 Beluga W	0.0194	0.0481	-0.0073	-0.0267	-0.0008	-0.0107	
15 Beluga James	-0.0015	0.0189	-0.0028	-0.0033	-0.0004	-0.0088	
16 Seabirds	-0.0025	-0.0018	0.0007	-0.0149	-0.0044	-0.0073	
17 Arctic Char	-0.0004	0.0008	-0.0006	-0.0018	-0.0001	-0.0012	
18 Atlantic Salmon	-0.0057	-0.0039	0.0003	-0.0167	0.0024	0.0019	
19 Gadiformes	0.0237	0.0325	-0.0038	0.0955	-0.0130	0.0138	
20 Sculpins/ Zoar- cids	0.0061	0.0125	-0.0012	0.0574	-0.0089	-0.0153	
21 Capelin	0.0603	0.0523	-0.0131	0.0412	0.0002	-0.0188	
22 Sandlance	0.0555	0.0243	-0.0101	-0.0197	-0.0015	-0.0122	
23 Sharks/Rays	0.0000	0.0023	-0.0003	-0.0008	-0.0001	-0.0004	
24 Other Marine Fish	0.0146	0.0165	-0.0037	0.0490	0.0149	0.0292	
25 Brackish Fish	0.0007	0.0024	-0.0002	0.0058	0.0000	-0.0008	
26 Cephalopods	-0.0135	-0.0046	0.0024	0.0182	0.0036	0.0016	
27 MacroZoopl.	0.0042	0.0043	-0.0113	0.0235	0.0035	0.0005	
28 Euphausiids	0.0169	0.0182	0.0720	0.0220	0.0030	-0.0028	
29 Copepods	0.0117	0.0118	0.1960	-0.0064	-0.0045	-0.0110	
30 Crustaceans	0.0346	0.0269	-0.0015	0.0683	-0.0746	-0.0722	
31 Other Meso- Zoopl.	-0.0138	-0.0135	-0.0624	-0.0239	0.0227	0.0259	
32 MicroZoopl.	0.0018	0.0009	-0.0023	-0.0014	0.0113	0.0094	
33 Marine Worms	-0.0046	0.0036	-0.0028	0.0081	0.0247	0.0427	
34 Echinoderms	0.0067	0.0032	-0.0027	0.0047	0.0779	0.0336	
35 Bivalves	-0.0081	0.0027	0.0072	0.0230	0.1540	0.2130	
36 Other Benthos	0.0135	0.0110	0.0212	0.0121	-0.0155	-0.0280	
37 Primary Produc- tion	0.0331	0.0274	0.1130	0.0233	0.0062	0.0000	
38 Ice Algae	0.0131	0.0149	0.0335	0.0329	0.0183	0.0236	
39 Ice Detritus	0.0082	0.0179	0.0158	0.0474	0.1360	0.1620	
40 Pelagic Detritus	0.0100	0.0082	0.0075	0.0117	-0.0046	-0.0055	
41 H: SH Polar Bear	0.0111	0.0125	-0.0018	-0.0037	-0.0005	0.0690	
42 H: WHB Polar Bear	0.0200	0.0155	-0.0022	-0.0084	0.0081	-0.0058	
43 H: FB Polar Bear	-0.3470	0.0088	-0.0012	-0.0041	-0.0003	-0.0032	
44 H: Killer whale	-0.0036	-0.4920	0.0726	0.0630	0.0109	0.0937	
45 H: Bowhead	0.0000	-0.0052	-0.4250	0.0007	0.0001	0.0010	
46 H: Narwhal	0.0005	-0.0162	0.0024	-0.4310	0.0001	0.0034	
47 H: N Walrus	0.0002	-0.0066	0.0010	0.0019	-0.4730	0.0033	
48 H: S Walrus	0.0237	0.0052	-0.0004	-0.0078	-0.0002	-0.3080	
49 H: Beluga E	0.0003	-0.0018	0.0003	0.0014	-0.0001	0.0005	
50 H: Beluga W	-0.0057	-0.0140	0.0021	0.0078	0.0002	0.0031	
51 H: Beluga S	0.0003	-0.0037	0.0005	0.0006	0.0001	0.0017	
52 H: Sealing	-0.0497	-0.0268	0.0036	0.0112	0.0013	0.0120	
53 H: Bird Hunting	0.0000	0.0000	0.0000	0.0002	0.0001	0.0001	
54 H: Fishing	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	

Table Continued on Next Page

Appendix F. Hudson Bay Mixed Trophic Impacts

Table F.1 Continued

Impacting/Impacted	H: Beluga W	H: Beluga S	H: Sealing	H: Bird Hunting	H: Fishing
1 Polar Bear WHB	-0.1500	0.0273	-0.0626	0.0038	0.0319
2 SH Polar Bear	0.0103	-0.2840	-0.0371	0.0003	0.0044
3 Polar Bear Foxe	-0.0474	0.0120	-0.0330	0.0015	0.0117
4 Killer Whale	-0.0381	-0.0383	0.0121	0.0003	0.0026
5 Narwhal	-0.0038	-0.0022	-0.0014	-0.0008	-0.0062
6 Bowhead	-0.0007	-0.0008	0.0001	-0.0001	0.0000
7 Walrus N	-0.0015	-0.0002	-0.0003	-0.0004	-0.0016
8 Walrus S	0.0409	0.0481	-0.1270	0.0041	0.0271
9 Bearded Seal	-0.0274	-0.0278	0.2310	0.0003	-0.0026
10 Harbour Seal	-0.0019	-0.0014	0.0006	-0.0008	-0.0023
11 Ringed Seal	-0.1380	-0.1640	0.3950	-0.0142	-0.0950
12 Harp seal	-0.0084	-0.0135	0.0151	-0.0008	0.0006
13 Beluga E	-0.0010	-0.0017	-0.0008	-0.0004	-0.0017
14 Beluga W	0.7290	-0.0250	-0.0231	-0.0107	-0.0964
15 Beluga James	-0.0026	0.8160	-0.0032	-0.0008	-0.0004
16 Seabirds	-0.0271	-0.0331	-0.0136	0.4790	-0.0718
17 Arctic Char	0.0307	-0.0045	-0.0025	0.0083	0.3490
18 Atlantic Salmon	-0.0072	-0.0106	-0.0122	-0.0077	-0.0440
19 Gadiformes	0.0634	-0.0131	0.0587	-0.0061	0.1300
20 Sculpins/ Zoar- cids	-0.0037	-0.0345	0.0167	0.0044	0.1560
21 Capelin	0.0971	0.3330	0.1150	0.0555	0.0651
22 Sandlance	-0.0388	-0.0639	0.1280	0.0073	0.0269
23 Sharks/Rays	-0.0002	-0.0002	0.0000	0.0000	0.0000
24 Other Marine Fish	0.0136	-0.0330	0.0320	0.0127	0.0586
25 Brackish Fish	0.0245	-0.0084	-0.0010	0.0439	0.0161
26 Cephalopods	0.0102	0.0117	-0.0329	0.0305	-0.1130
27 MacroZoopl.	0.0009	0.0035	0.0061	0.0658	0.0047
28 Euphausiids	0.0650	0.1010	0.0294	0.0299	-0.0131
29 Copepods	0.0403	0.0589	0.0216	-0.0014	0.0388
30 Crustaceans	0.0395	0.0565	0.0955	-0.0063	-0.0114
31 Other Meso- Zoopl.	-0.0391	-0.0581	-0.0322	-0.0010	0.0192
32 MicroZoopl.	-0.0019	-0.0020	0.0012	0.0196	0.0087
33 Marine Worms	0.0179	0.0084	-0.0042	-0.0030	0.0255
34 Echinoderms	-0.0116	-0.0245	0.0073	0.0044	0.0268
35 Bivalves	0.0096	0.0042	-0.0303	0.0390	0.0155
36 Other Benthos	0.0566	0.0481	0.0156	-0.0024	0.0250
37 Primary Produc- tion	0.0497	0.0872	0.0675	0.0463	0.0724
38 Ice Algae	0.0336	0.0194	0.0258	0.0165	0.0541
39 Ice Detritus	0.0564	0.0314	0.0031	0.0253	0.0736
40 Pelagic Detritus	0.0110	0.0201	0.0217	0.0353	0.0075
41 H: SH Polar Bear	-0.0075	0.2080	0.0272	-0.0002	-0.0032
42 H: WHB Polar Bear	0.0918	-0.0167	0.0382	-0.0023	-0.0195
43 H: FB Polar Bear	0.0338	-0.0086	0.0236	-0.0011	-0.0084
44 H: Killer whale	0.0381	0.0383	-0.0121	-0.0003	-0.0026
45 H: Bowhead	0.0005	0.0006	0.0000	0.0001	0.0000
46 H: Narwhal	0.0029	0.0017	0.0011	0.0006	0.0048
47 H: N Walrus	0.0013	0.0002	0.0003	0.0004	0.0014
48 H: S Walrus	-0.0179	-0.0210	0.0556	-0.0018	-0.0119
49 H: Beluga E	0.0008	0.0015	0.0007	0.0003	0.0015
50 H: Beluga W	-0.2120	0.0073	0.0067	0.0031	0.0280
51 H: Beluga S	0.0005	-0.1580	0.0006	0.0002	0.0001
52 H: Sealing	0.0284	0.0325	-0.1280	0.0020	0.0134
53 H: Bird Hunting	0.0004	0.0005	0.0002	-0.0079	0.0012
54 H: Fishing	0.0000	0.0000	0.0000	0.0000	0.0000

Appendix G

Hudson Bay Monte Carlo CV Values

Appendix G. Hudson Bay Monte Carlo CV Values

Table G.1: Coefficient of Variation (CV) values used for Monte Carlo routine; Biomass, Production/Biomass (P/B), Ecotrophic Efficiency (EE) and Biomass Accumulation (BA).

Functional Group	Biomass (CV)	P/B (CV)	EE (CV)	BA (CV)
Polar Bear WHB	0.15	0.25	0.1	0.05
SH Polar Bear	0.15	0.25	0.1	0.05
Polar Bear Foxe	0.15	0.25	0.1	0.05
Killer Whale	0.15	0.1	0.1	0.05
Narwhal	0.15	0.1	0.1	0.05
Bowhead	0.4	0.1	0.1	0.15
Walrus N	0.25	0.1	0.1	0.05
Walrus S	0.25	0.1	0.1	0.05
Bearded Seal	0.25	0.1	0.1	0.05
Harbour Seal	0.25	0.1	0.1	0.05
Ringed Seal	0.25	0.1	0.1	0.05
Harp seal	0.25	0.1	0.1	0.05
Beluga E	0.15	0.1	0.1	0.15
Beluga W	0.15	0.1	0.1	0.15
Beluga James	0.15	0.1	0.1	0.05
Seabirds	0.4	0.3	0.1	0.05
Arctic Char	0.1	0.2	0.1	0.05
Atlantic Salmon	0.1	0.2	0.1	0.05
Gadiformes	0.1	0.2	0.1	0.05
Sculpins/ Zoarcids	0.1	0.2	0.1	0.05
Capelin	0.1	0.2	0.1	0.05
Sandlance	0.1	0.2	0.1	0.05
Sharks/Rays	0.1	0.2	0.1	0.05
Other Marine Fish	0.1	0.2	0.1	0.05
Brackish Fish	0.1	0.25	0.1	0.05
Cephalopods	0.25	0.3	0.1	0.05
MacroZooplankton	0.25	0.2	0.1	0.05
Euphausiids	0.15	0.2	0.1	0.05
Copepods	0.15	0.2	0.1	0.05
Crustaceans	0.15	0.2	0.1	0.05
Other MesoZooplankton	0.15	0.2	0.1	0.05
MicroZooplankton	0.25	0.35	0.1	0.05
Marine Worms	0.1	0.25	0.1	0.05
Echinoderms	0.1	0.25	0.1	0.05
Bivalves	0.1	0.25	0.1	0.05
Other Benthos	0.1	0.25	0.1	0.05
Primary Production	0.15	0.1	0.1	0.05
Ice Algae	0.15	0.1	0.1	0.05

Appendix H

Hudson Bay Monte Carlo Results

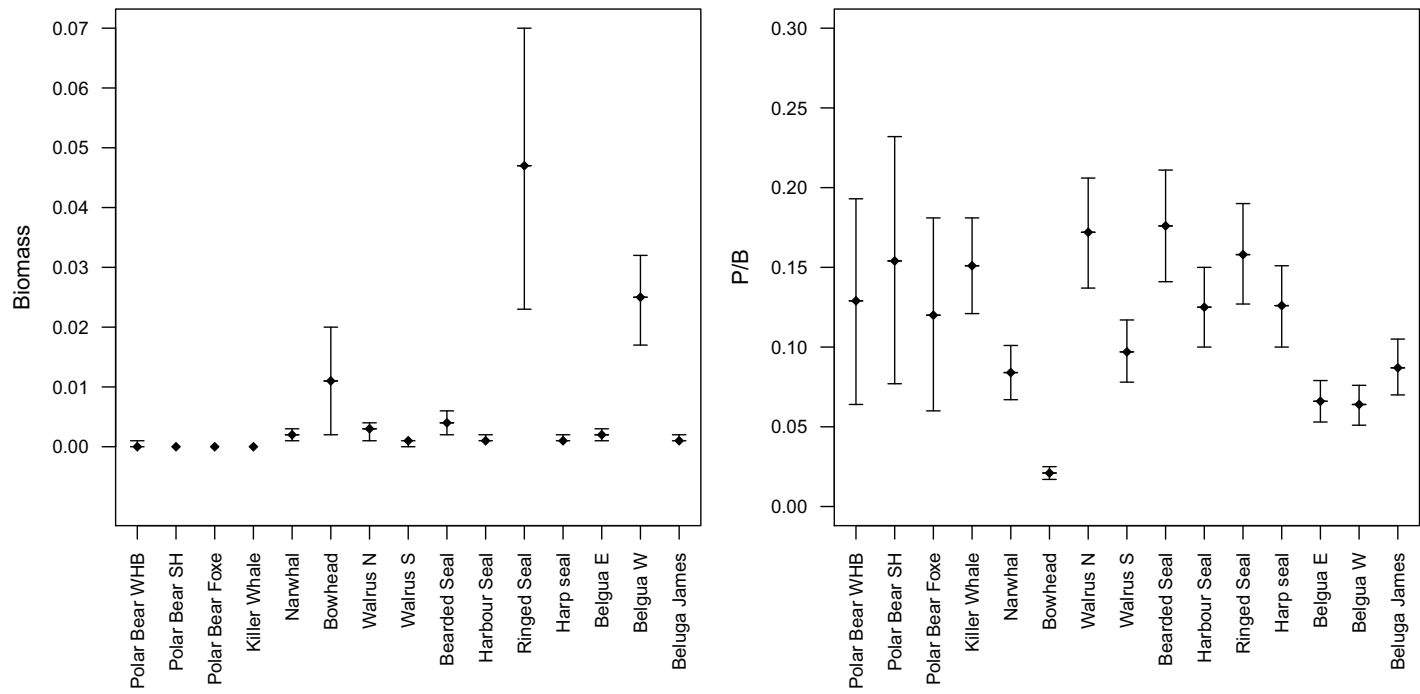


Figure H.1: Monte Carlo results for estimates of biomass ($t \cdot km^{-2}$) and P/B (y^{-1}) for marine mammal groups.

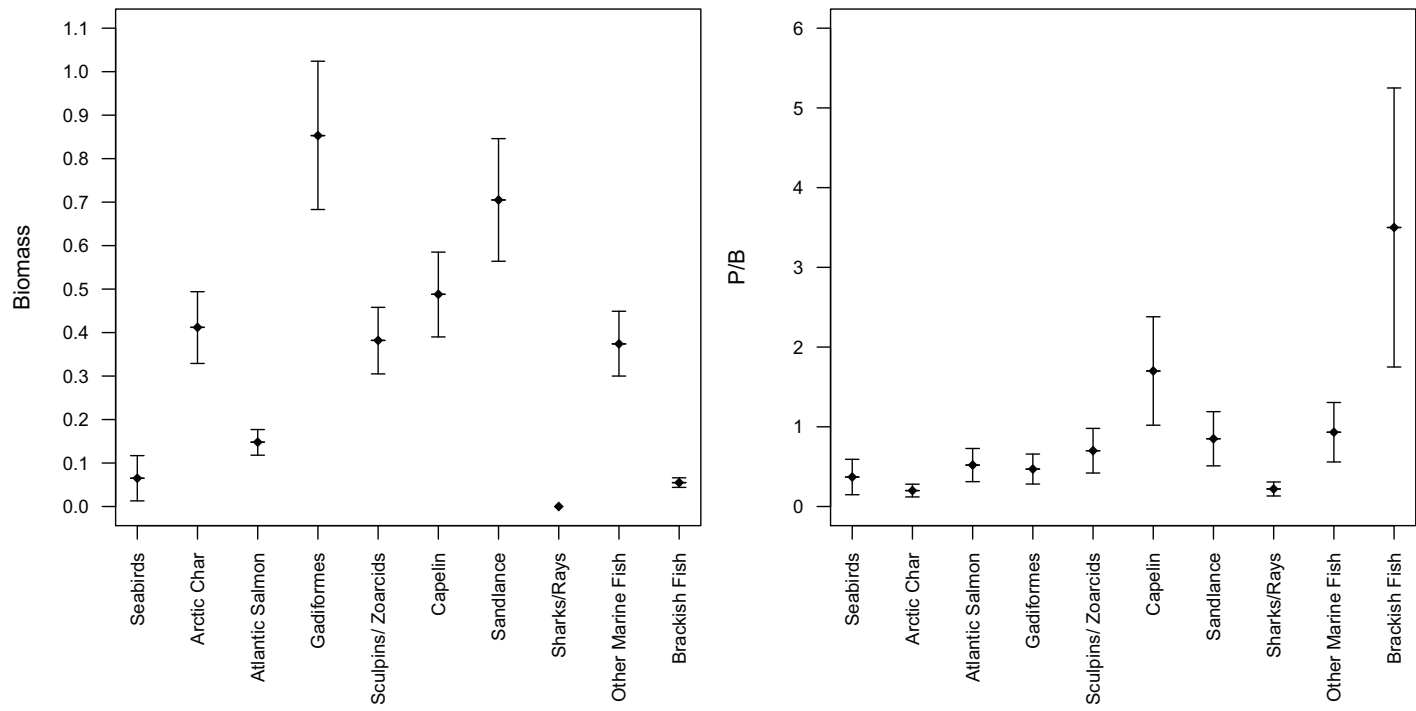


Figure H.2: Monte Carlo results for estimates of biomass ($t \cdot km^{-2}$) and P/B (y^{-1}) for fish groups.

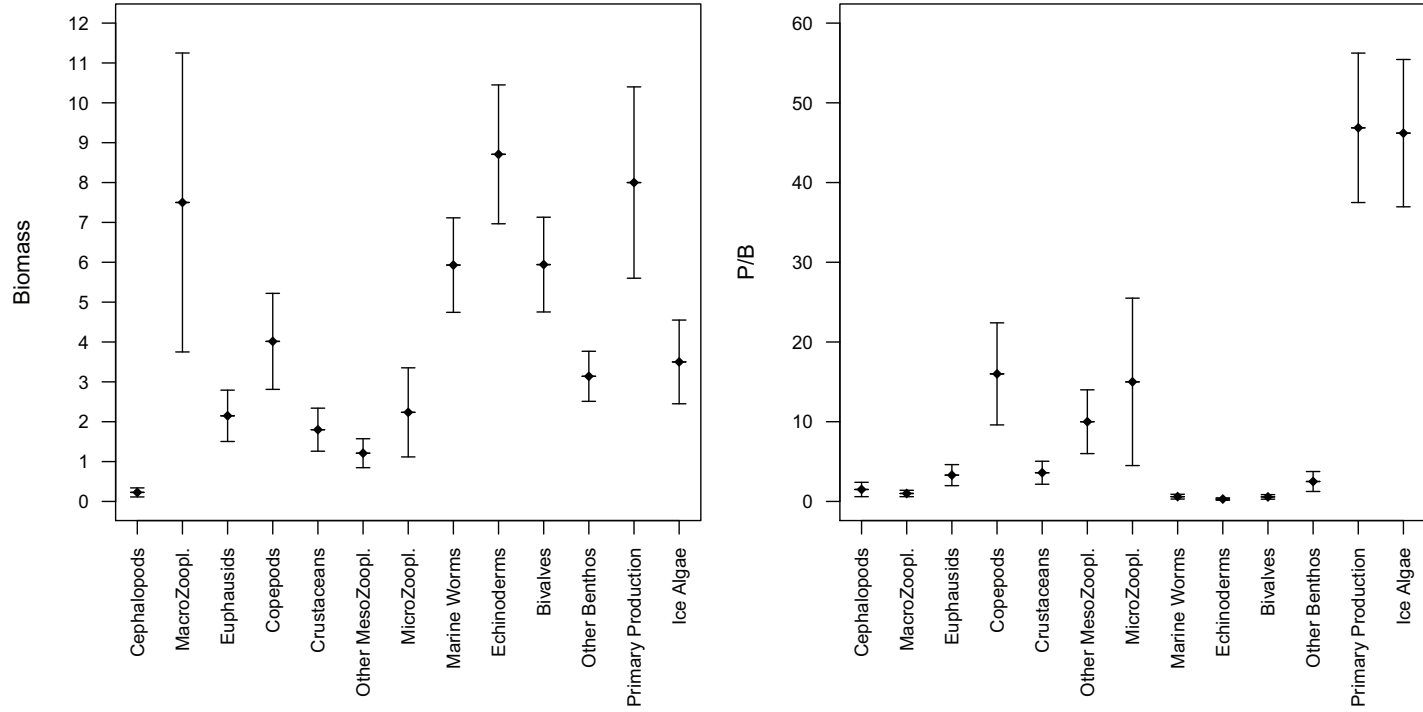


Figure H.3: Monte Carlo results for estimates of biomass ($t \cdot km^{-2}$) and P/B (y^{-1}) for zooplankton and primary producer groups.

Appendix I

Hudson Bay Ecosim Biomass Trends by Species

Appendix I. Hudson Bay Ecosim Biomass Trends by Species

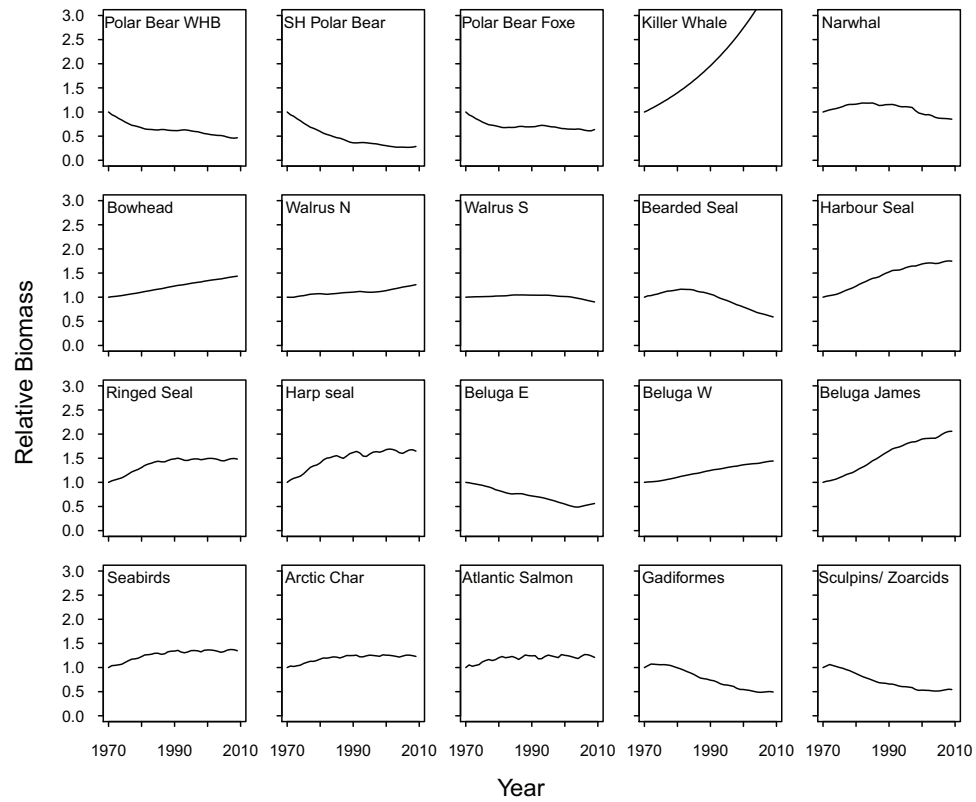


Figure I.1: Biomass trends from 1970-2010 as scaled to 1970 biomass value by functional group

Appendix I. Hudson Bay Ecosim Biomass Trends by Species

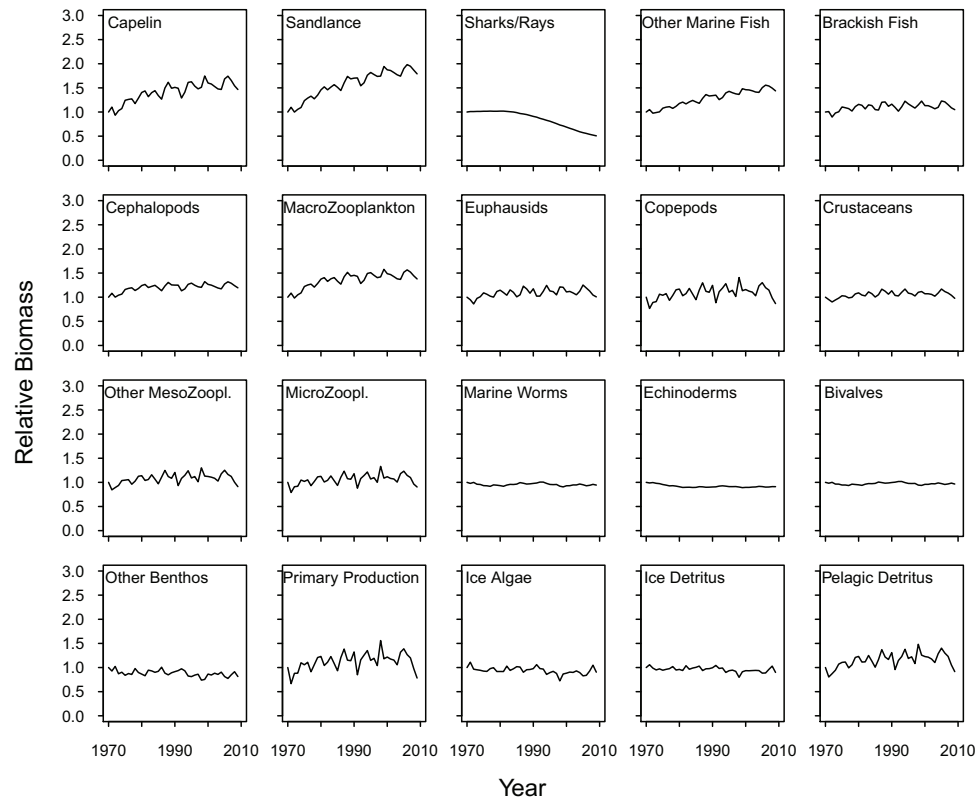


Figure I.2: Biomass trends from 1970-2010 as scaled to 1970 biomass value by functional group

Appendix J

Antarctic Peninsula Ecosystem Model Parameters and Details

J.1 Model Parameters by Functional Group

Functional groups were created with a focus on krill, salps, and the top predators primarily dependent on krill. Marine mammals and penguins were given functional groups for each species identified in the model area, while fish were grouped together based on life history and diet. Pelagic and benthic surveys provided information on invertebrate species, therefore allowing for greater detail of these species groups.

Marine Mammals

Table J.1: Estimates of cetaceans from three Southern Ocean circumpolar surveys as presented in Branch and Butterworth (2001).

Species	First Circumpolar (1978-1984)	Second Circumpolar (1985-1991)	Third Circumpolar (1991-1998)
Blue Whale	440	550	1100
Fin Whale	2100	2100	5500
Sperm Whale	5400	10000	8300
Humpback Whale	7100	9200	9300
Killer Whale	91000	27000	25000

The marine mammals included in this model are the species which have been identified to inhabit the region on a yearly basis, or make a seasonal

migration back to the region every year. For the purpose of the model the marine mammal groups each represent an individual species. Biomass for each group was determined by using the average weight per individual as determined by Trites and Pauley (1998), compared to distribution and abundance information for each species. Southern Ocean abundance of cetacean species are found in table J.1 as summarized by Branch and Butterworth (2001).

Mortality rates were calculated for each species using the life table from Barlow and Boveng (1991), where life history patterns and longevity are used to calculate natural mortality. Full equations are available in appendix B, with longevity listed in table J.2. These values were used as the P/B ratio for the first year of the model, as there is no hunting mortality on marine mammal species within the model area.

Consumption (Q/B) was calculated using an empirical equation (Eq. J.1) from Hunt et al. (2000), where E is the energy required per day (Kcal/day), M is the mean body weight (in Kg) and a is a coefficient representing each group of marine mammals ($a=320$ for otariids, 200 for phocids, 192 for mysticetes, 317 for odontocetes, and 320 for sea otters). The energy requirement was compared to energy consumed, based on energy content in the diet (Cauffope and Heymans, 2005), in order to get the Q/B ratio. Table J.2 shows calculated values, values from literature, and values used in the model.

$$E = aM^{0.75} \tag{J.1}$$

Table J.2: Published and calculated marine mammal parameters used in the model.

	Functional Group	Mean Weight (Kg)	Longevity (Years)	Reference	Natural Mortality [‡]	Model P/B	Calc. Q/B*	Model Q/B
1	Killer Whales	2280.5 [†]	50	Trites and Pauley (1998)	0.057	0.05	7.39	11
2	Leopard Seal	464	26	Australian Antarctic Division (2008)	0.102	0.12	9.95	8.1
3	Ross Seal	145.5	24	Skinner and Klages (1994)	0.125	0.13	15.3	15.3
4	Weddell Seal	158	13.5 [†]	Trites and Pauley (1998)	0.175	0.17	13.88	13.88
5	Crabeater Seal	206	36	Carey and Judge (2001)	0.083	0.09	15.86	15.86
6	Antarctic Fur Seals	26.7 [†]	13.5	Trites and Pauley (1998)	0.175	0.175	33.18	25
7	Elephant Seals	435 [†]	15	Trites and Pauley (1998)	0.165	0.165	10.37	10.37
8	Sperm Whales	18518.5 [†]	69	Trites and Pauley (1998)	0.043	0.034	7.33	7.33
9	Blue Whales	102736.5 [†]	100	Trites and Pauley (1998)	0.032	0.032	3.53	3.53
10	Fin Whales	55590 [†]	98	Trites and Pauley (1998)	0.035	0.035	4.12	4.12
11	Minke Whales	6566 [†]	47	Trites and Pauley (1998)	0.064	0.064	6.34	6.34
12	Humpback Whales	30408 [†]	75	Trites and Pauley (1998)	0.04	0.04	4.54	4.12

[†] Mean weights taken from Trites and Pauley (1998) were averaged for males and females.

[‡] Natural mortality was calculated from Barlow and Boveng (1991), see appendix B for equations.

* Calculated Q/B values were obtained using Eq.J.1.

Killer Whales

(*Orcinus orca*) Recently in the Antarctic, three ecotypes have been identified which appear to be similar to the killer whales residing in the Pacific Northwest. In the Antarctic Peninsula types A (minke whale specialists) and B (seal specialists) have been observed, while type C is primarily observed off east Antarctica and has been observed to consume Antarctic toothfish; *Disostichus mawsoni* (Pitman and Ensor, 2003; Waples and Clapham, 2004). For this model it is assumed that killer whales are year round inhabitants based on observations in the winter at other locations in the Antarctic (Gill and Thiele, 1997). Based on surveys in table J.1 from Branch and Butterworth (2001), the biomass from the first, second and third surveys would have been 0.0058, 0.0017, 0.0016 $t \cdot km^{-2}$, assuming an even distribution of whales in the Southern Ocean. However, more localized surveys present much lower estimates of killer whales (Childerhouse, 2005; Secchi et al., 2006). The biomass for the first year was set to 0.001 $t \cdot km^{-2}$. The production/ biomass ratio was calculated to be $0.057y^{-1}$, but was lowered to $0.05y^{-1}$ to balance the model. The Q/B ratio was set to $11y^{-1}$, which is higher than the calculated transient Orca value in Guenette (2005). However it was used being that the majority of whales sighted in the area fed on marine mammals (Pitman and Ensor, 2003). Based on observations of marine mammal eating killer whales, the diet was set to: 4% leopard seals, 2% Ross seals, 16% Weddell seals, 19% crabeater seals, 9% Antarctic fur seals, 0.1% blue whales, 0.5% fin whales, 34.4% minke whales, 7% humpback whales, 6% penguins (1% Gentoo, 2% Chinstrap, 1% Macaroni, 3% Adelie), and 1% flying birds.

Leopard Seal

(*Hydrurga leptonyx*) Leopard seals are year round inhabitants, with their diet being dominated by krill and fish in the winter then shifting to penguins and other marine mammals in the summer (Lowry et al., 1998; Walker et al., 1998; Hall-Aspland and Rogers, 2004). Estimates of leopard seals range from 0.5-1.1 seals $\cdot km^{-2}$ for the Weddell Sea (Van Franeker et al., 1997),

to $0.1 \text{ seals} \cdot \text{km}^{-2}$ for the Amundsen and Bellingshausen Seas (Gilbert and Erickson, 1977). The biomass for the model was set to $0.00576t \cdot \text{km}^{-2}$. This is lower than other areas, as leopard seals are associated with pack ice, and the other areas sampled have higher levels of year round sea ice. The P/B was increased slightly from the calculated value to 0.12 y^{-1} to account for killer whale predation, and the Q/B value was lowered slightly to 8.1 ^{-1} to balance the penguin groups.

The average diet was set to: 0.5% Ross seal, 1.5% Weddell seal, 7% crabeater seal, 7% Antarctic fur seal, 1% elephant seal, 1.5% emperor penguins, 1% Gentoo penguins, 1% chinstrap penguins, 3% macaroni penguins, 10% Adelie penguins, 4% flying birds, 15% cephalopods, 2% other icefish, 1% large notothenioids, 1% small notothenioids, 1% shallow demersals, 0.5% deep demersals large, 1% deep demersals small, 1% myctophids, 1% other pelagics, 1% *C. gunnari*, 1% *P. antarcticum*, 1% *N. gibberifrons*, 19% adult krill, and 17% sub-adult krill (Penney and Lowry, 1967; Muller-Schwarze and Muller-Schwarze, 1975; Siniff and Stone, 1985; Walker et al., 1998; Hiruki et al., 1999; Hall-Aspland and Rogers, 2004).

Ross Seal

(*Ommatophoca rossii*) The Ross seal lives deep within the pack ice and is one of the least studied seals. They are known to feed primarily on fish and squid, with dive depths mostly correlating to pelagic feeding with some benthic dives (Skinner and Klages, 1994; Bengston and Stewart, 1977). They are mostly found in interior pack ice zones in places such as the Ross Sea; $0.6 \text{ animals} \cdot \text{km}^{-2}$ Ackley et al. (2003), with a smaller portion found in the pelagic areas (Gilbert and Erickson, 1977). The biomass for the peninsula was set to nearly half of the Ross Sea population, or $0.0042t \cdot \text{km}^{-2}$. The P/B ratio was set to the calculated value 0.13y^{-1} , and the calculated value of 15.3y^{-1} was used for Q/B.

The diet for Ross seals was set to: 46% cephalopods, 1.5% other icefish, 4.5% large notothenioids, 1% small notothenioids, 0.1% shallow demersals, 0.1% deep demersals large, 0.5% deep demersals small, 2% myctophids, 1%

other pelagics, 2% *C. gunnari*, 14% *P. antarcticum*, 3% *N. gibberifrons*, 4% mollusca, 1.5% salps, 0.5% cnidarians, 2.9% arthropod crustacea, 0.5% other arthropods, 1% worms, 6% adult krill, and 7.9% sub adult krill (Knox, 1994; Skinner and Klages, 1994; Casaux et al., 1997).

Weddell Seal

(*Leptonychotes weddellii*) Weddell seals have a circumpolar distribution and are known to inhabit the pack or fast ice near the continent, and haul out on the islands near the peninsula (Riffenburg, 2006). Biomass for the Southern Ocean averaged $0.005t \cdot km^{-2}$ (Laws, 1977), and 0.021 to $0.12t \cdot km^{-2}$ for the Amundsen and Bellingshausen Seas for the 1970's and 1994 respectively (Gilbert and Erickson, 1977; Gelatt and Siniff, 1999). The biomass was set to $0.021t \cdot km^{-2}$ for the model. The P/B was increased from the calculated value to $0.17y^{-1}$ to account for predation by killer whales, and the Q/B was set to the calculated value of $13.88y^{-1}$.

The diet of Weddell seals contains cephalopods ranging from 2-65%, molluscs 1-65%, and crustaceans 2-23%, with various fish and cephalopods contributing greatly to their diet (Clarke and MacLeod, 1982; Green and Burton, 1987; Casaux et al., 1997; Burns et al., 1998). The diet composition was set to: 29% cephalopods, 0.5% other icefish, 3% large notothenioids, 1.5% small notothenioids, 0.1% deep demersals large, 0.5% deep demersals small, 2% myctophids, 1% other pelagics, 2% *C. gunnari*, 23% *P. antarcticum*, 3% *N. gibberifrons*, 18% mollusca, 6.4% arthropod crustaceans, 0.5% other arthropods, 1% worms, 3.5% adult krill, 5% sub-adult krill (Green and Burton, 1987; Casaux et al., 1997; Burns et al., 1998).

Crabeater Seal

(*Lobodon carcinophagus*) Crabeater seals are generally found within the pack ice and are the most abundant pinniped species in the Antarctic (Riffenburg, 2006). Although crabeater seals have been known to consume some fish, they feed almost exclusively on krill, demonstrating a specialized adaptation in their teeth to strain the water from large mouthfuls of krill (Lowry et al.,

1998). Estimates of crabeater seals from the Amundshausen and Bellingshausen Seas are as high as $3.32 \text{ seals} \cdot \text{km}^{-2}$ in 1994 (Gelatt and Siniff, 1999), with estimates on pack ice averaging $0.76 \text{ seals} \cdot \text{km}^{-2}$ from the 1970s (Gilbert and Erickson, 1977). The density of seals in the pack ice in the Weddell Sea ranged from 0.45 to $1 \text{ seal} \cdot \text{km}^{-2}$ (Van Franeker et al., 1997). A density of $0.8 \text{ seals} \cdot \text{km}^{-2}$ or $0.164t \cdot \text{km}^{-2}$ was used for the Antarctic Peninsula. The P/B for crabeater seals was increased from the calculated value of 0.083 to 0.09y^{-1} to balance the model, and the Q/B was set to the calculated value of 15.86y^{-1} . The diet for crabeater seals was set to: 2.5% cephalopods, 0.5% myctophids, 0.25% other pelagics, 2% *P. antarcticum*, 3% mollusca, 1% salps, 45% adult krill, 40% sub-adult krill, 5% macro-zooplankton, 0.7% micro-zooplankton (Lowry et al., 1998; Bredeesen, 2003; Efran and Pitcher, 2005).

Antarctic Fur Seals

(*Arctocephalus gazella*) There is a large proportion of fur seals within the Scotia Sea as South Georgia is one of the main breeding grounds. However, seals do travel between South Georgia and the Peninsula, and there are a number of seals which do breed near the peninsula (Boyd et al., 1998). The biomass at South Georgia was estimated to be just over 1 million seals in the 1980s (Doidge and Croxall, 1985) or $0.028 \cdot \text{km}^{-2}$. The same value was used for the model biomass. The P/B ratio used as calculated from the life table, 0.175y^{-1} , was comparable to the estimate 0.16y^{-1} for northern fur seals (Wikens and York, 1997; Guenette, 2005). The calculated Q/B of 33.18y^{-1} was lowered to 25y^{-1} to reduce the predation mortality on krill and fish species.

Antarctic fur seals primarily consume krill, with fish being an important food source to males during the winter. Yearly estimates of fish contribution to the diet from a variety of species ranges from 5-50% at South Georgia Doidge and Croxall (1985). North et al. (1983), Reid (1995), and Reid and Arnould (1996) provide individual species contribution of fish to the diet. Cephalopods in the diet at South Georgia average 12% a year, with krill esti-

mates as high as 92% (Doidge and Croxall, 1985; Daneri and Carlini, 1999). The average yearly diet was set to: 18% cephalopods, 1% other icefish, 2.4% large notothenioids, 1% small notothenioids, 0.1% shallow demersals, 0.1% deep demersals large, 0.25% deep demersals small, 1% myctophids, 1% other pelagics, 2.5% *C. gunnari*, 3% *N. gibberifrons*, 34.8% adult krill. 34.9% sub-adult krill (North et al., 1983; Doidge and Croxall, 1985; Reid, 1995; Reid and Arnould, 1996)

Southern Elephant Seals

(*Mirounga leonina*) The Southern elephant seal, the largest of the Antarctic seals, is capable of diving up to 900 meters in order to forage for food that is mostly comprised of cephalopods (McConnell et al., 1992). Population size before the 1960s was noted as 315,100 seals for the area including South Georgia, Falkland Islands, Patagonia, South Shetland Island, Bouvet Island, and Gough Island (Laws, 1960). This accounts for almost half of the total estimated population for the Southern Ocean at 600,000 (Laws, 1977) or $0.0026t \cdot km^{-2}$, assuming equal distribution. Later studies from Elephant Island (South Shetland Islands) indicated only 300 animals resided on the island (Hunt, 1973). The biomass for the model area was set to $0.00647 \cdot km^{-2}$, assuming 10,000 of the 315,100 seals from the 1960s were located in the model area. The P/B and Q/B calculated values of $0.165y^{-1}$ and $10.37y^{-1}$ respectively were used for the model.

Dive profiles of elephant seals indicate benthic feeding, with shallower dives translating to travel time between feeding grounds (McConnell et al., 1992). However, fish in the diet at King George Island at the Antarctic Peninsula is dominated by myctophids; a partially pelagic species, followed by notothenioids and icefish (Daneri and Carlini, 2002). A higher proportion of seals have a fish dominated diet in the winter, indicative of shelf foraging, while squid dominate the diets in the summer, indicative of pelagic foraging (Bradshaw et al., 2003). Overall, squid are the most important contributor to the diet at South Georgia (Rodhouse et al., 1992). The diet composition was set to: 72% cephalopods, 1.5% other icefish, 1.5% toothfish, 0.1% large

notothenioids, 8% myctophids, 1% other pelagics, 2% *P. antarcticum*, 7.9% mollusca, 1% arthropod crustaceans, 3% adult krill, and 2% sub-adult krill (McConnell et al., 1992; Rodhouse et al., 1992; Daneri and Carlini, 2002; Bradshaw et al., 2003).

Sperm Whales

(*Physeter macrocephalus*) Early estimates by Laws (1977) suggested the sperm whale population in the Southern Ocean was roughly 43,000 whales, however more recent studies have estimated the population to be in the 5,400-10,000 range below 60° S (Branch and Butterworth, 2001). Whether these are differences in sampling or changes to the population remain unknown. Density at South Georgia ranged from 0.00013 to 0.00019 whales·km⁻² for 1999 and 2000 respectively (Leaper et al., 2000), leading to a biomass of 0.0024 to 0.0035t·km⁻². Biomass was assumed to be higher at the peninsula than South Georgia due to cooler deeper waters and was set to 0.005t·km⁻² for the start of the model. The P/B was lowered from the calculated value of 0.043y⁻¹ to 0.034y⁻¹ to balance the model. The calculated Q/B value of 7.33y⁻¹ was used. The diet of sperm whales is thought to be based in deep water to coincide with their ability to dive at depths for long periods of time. Squid makes up the majority of the diet, with fish and invertebrates taken opportunistically (Knox, 1994; Pauly et al., 1998b). Based on this information the diet was set to: 75.2% cephalopods, 1.5% toothfish, 1% deep demersals large, 2% deep demersals small, 3% mollusca, 2% salps, 0.5% hemichordata, 0.5% brachiopoda, 0.5% bryozoa, 1.5% cnidarians, 0.1% crustaceans, 1% worms, 0.4% holothuroidea, 5.5% adult krill, and 5.3% sub-adult krill.

Baleen Whales

For the 4 groups of baleen whales in the model, adjustments have been made to the peak summer biomass in order to correct for the fact that these animals do not inhabit the model area year round. During the summer months, these whales migrate great distances in order to feed on shifting

populations of krill and then travel to their winter breeding grounds. Most species feed in the Antarctic Peninsula region for only three to six months per year, but their impact on the ecosystem is related to their food intake, and is not strictly proportional to the amount of time spent in the area. Growth of baleen plates and trophic signatures have been correlated with feeding time in high latitude areas for southern right whales (Best and Schell, 1996). This study demonstrates how important the summer feeding season is to the growth of baleen whales, and how it accounts for a majority of the food consumed annually by these animals. However, bowhead whales in the northern hemisphere, especially juveniles, have been shown to feed heavily in summer and winter indicating they require food sources outside of their summer feeding areas (Schell et al., 1989). In order to account for the fact that most, but not all of their annual food intake comes from the peninsula, the biomass of the baleen whales has been adjusted to be 75% of their peak summer biomass.

Blue Whales (*Balaenoptera musculus*) Blue whales migrate to the peninsula every austral summer in order to take advantage of the high krill biomass, which accounts for most of their annual food intake. Branch and Butterworth (2001) estimated the population in the Southern Ocean to be between 400-1100 whales based on three surveys taken over a 20 year period. However, the CCAMLR survey in 2000 only recorded 1 blue whale in the survey area of the peninsula region (Reilly et al., 2004), which did not include the entire model area. Based on the survey data, it was assumed an average of five whales would be present in the model area for the summer feeding months. The adjusted biomass¹⁹ for blue whales is $0.0005t \cdot km^{-2}$. The P/B and Q/B were set to the calculated values in table J.2.

Blue whale diets consists of small amounts of cephalopods, myctophids, with large amounts of krill (Laws, 1977; Armstrong and Siegfried, 1991; Knox, 1994; Tamura and Konishi, 2005). The diet for blue whales was assumed to be: 3% myctophids, 2% other pelagics, 3% *P. antarcticum*, 35% adult krill, 35% sub-adult krill, 2% macro-zooplankton, 5% micro-

¹⁹ Assuming 75% of the biomass for 5 whales

zooplankton and 15% copepods.

Fin Whales (*Balaenoptera physalus*) Fin whales are also only present in the model area during the summer. Estimates for the Southern Ocean range from 2100 to 5500 whales (Branch and Butterworth, 2001), with 56 whales estimated to be in the peninsula region (Reilly et al., 2004). For the model it was estimated that 50 whales inhabit the peninsula region for the summer months, giving a yearly average biomass of $0.003t \cdot km^{-2}$. The calculated P/B and Q/B values from table J.2 were used for the model. The diet for fin whales was set to a diet similar to blue whales in the area as they are believed to primarily target krill while likely consuming a small amount of fish and other organisms. Average annual diet was set to: 5% myctophids, 2% other pelagics, 3% *P. antarcticum*, 39% adult krill, 30% sub-adult krill, 5% macro-zooplankton, 6% micro-zooplankton and 10% copepods.

Minke Whales (*Balaenoptera bonaerensis*) The summering population of minke whales has been shown to range from 112 whales (Reilly et al., 2004) to 1544 whales for areas between South America and the Antarctic Peninsula (Williams et al., 2006). Abundance estimates for the western Weddell Sea were $0.04 \text{ whales} \cdot km^{-2}$ for areas south of the ice edge, with no whales found in areas north of the ice edge (Van Franeker et al., 1997). Based on this literature, the biomass of minke whales was set to $0.011t \cdot km^{-2}$ or 1500 whales present during the summer. This value was increased slightly to give a biomass of $0.065t \cdot km^{-2}$ in order to balance the model, as there are a large component of killer whales in the area. The calculated P/B and Q/B values were used for the model from table J.2. The diet for minke whales was set to: 0.5% cephalopods, 0.1% myctophids, 0.5% other pelagics, 0.5% *P. antarcticum*, 20% adult krill, 45% sub-adult krill, 5% macro-zooplankton, 15% micro-zooplankton and 13.4% copepods.

Humpback Whales (*Megaptera novaeangliae*) The population of humpback whales in the Southern ocean was estimated to be between 7100-9300 whales for the years 1978 to 1998 (Van Franeker et al., 1997). Based on

migrations of humpback and photo identification 1105 individual whales have been identified between their summer feeding grounds at the Antarctic Peninsula and their breeding grounds in western South America (Ecuador and Columbia) and Brazil, with 535 individuals sighted within the model area (Stevick et al., 2004). Others estimate 181 whales between the peninsula and South Georgia (Reilly et al., 2004), however this survey did not include all of area 48.1. The biomass for humpback whales was set to $0.02t \cdot km^{-2}$ which is based on 600 whales residing in the model area for the summer months. The calculated P/B of $0.04y^{-1}$ was used, however the Q/B was decreased slightly from $4.54y^{-1}$ to $4.12y^{-1}$ to balance the model.

In the summer, krill is a main staple of the diet, contributing up to 97% of the diet, with cephalopods and fish making up the rest (Laws, 1977; Knox, 1994). The diet was set to: 0.5% cephalopods, 1% myctophids, 0.5% other pelagics, 0.5% *P. antarcticum*, 37.5% adult krill, 35% sub-adult krill, 5% macro-zooplankton, 10% micro-zooplankton and 10% copepods.

Penguins

There are five species of penguins known to reside in the Antarctic Peninsula; the adelic, gentoo, chinstrap, emperor, and macaroni penguins. The emperor and adelic penguins have a circumpolar distribution, while, gentoo, macaroni and chinstrap penguins are found on sub-Antarctic islands and the peninsula is generally the only portion of the continent in which they reside. At PALMER station on Anvers Island, a US monitoring program has noted that before 1950 only adelic penguins were known to inhabit the region. Adelic populations are believed to have increased from the 1950s to the 1970s, when populations at certain areas began to decline (King George Island and Signy Island) (Croxall et al., 2002). However, since this time gentoo and chinstrap penguins have moved south in correlation with warming trends (Emslie et al., 1998). The gentoo population at Cierva Point on the peninsula has nearly doubled from 1954 to 1996 (Quintana and Cirelli, 2000). While it is unknown if these trends hold true across the entire model area, data from the PALMER station Long Term Ecological Research (LTER)

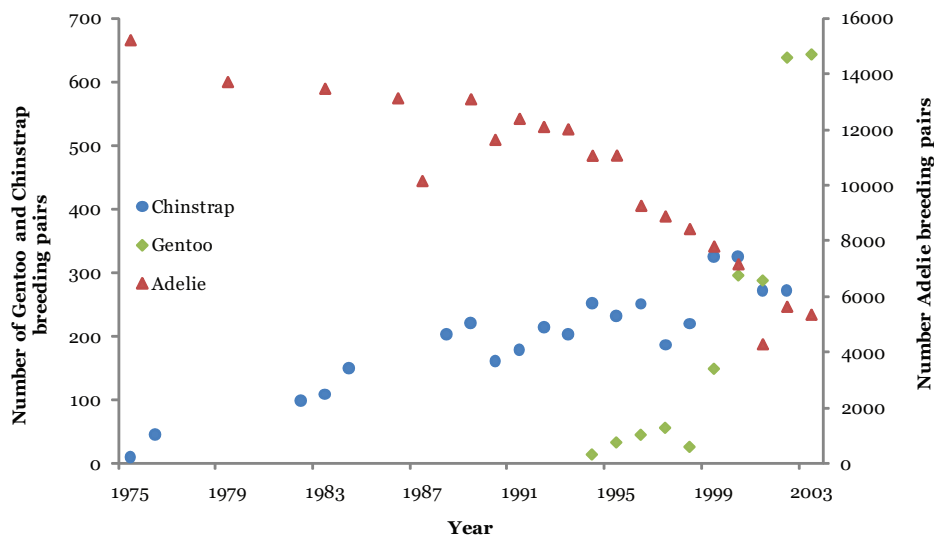


Figure J.1: Number of breeding pairs for Chinstrap, Gentoo, and Adelie penguins from surveys at PALMER station, Anvers Island, Antarctic Peninsula (Fraser, 2006).

dataset has been incorporated into the model (Figure J.1).

Surveys of various penguin rookeries at the south Shetland islands estimate populations of adelie, gentoo, and chinstraps at 65300, 12600, and 625000 breeding pairs respectively for the early 1980s (Trivelpiece et al., 1987)²⁰. These were considered conservative estimates, as the surveys did not cover the entire model area. A more comprehensive survey for adelie penguins identified higher abundance within inshore zones in 1986; up to $3.5 \text{ animals} \cdot \text{km}^{-2}$ (Whitehouse and Viet, 1994). Abundances of macaroni and emperor penguins were assumed based on their relative abundance compared to other penguin species, primarily adelie P/B ratios were assumed for most species, based on survival rates of adelie penguins and taking into account other factors such as size and longevity. An average mortality rate of 0.29y^{-1} was used based for adelie penguins on survivorship from 1968-

²⁰It should be noted that Trivelpiece et al. (2010) identify declines of all three species of penguins studied: Adelie, Chinstrap and Gentoo in a recent study and is compared with the model in the discussion.

1976 at colonies in eastern Antarctica (Ainley and DeMaster, 1980). Annual survival is higher in larger penguins, and has been shown to be higher in species that begin breeding later in life and have a higher longevity (Croxall and Davis, 1999). As chinstrap and macaroni penguins are slightly smaller than adelic penguins, with nearly the same lifespan, the P/B of both groups was set slightly higher at $0.3y^{-1}$. Emperor penguins have higher annual adult survival rates of 0.9 to $0.95y^{-1}$ (Bried et al., 1999; Croxall and Davis, 1999). As these were for adult survival, the population P/B was assumed to be $0.15y^{-1}$. Gentoo penguins fall between emperor and adelic penguins in size, therefore their P/B was assumed to be $0.2y^{-1}$. Consumption was calculated using two general equations J.2 and J.3 to calculate the basal metabolic rate (BMR) and field metabolic rate (FMR) for Sphenisciformes (Ellis and Gabrielsen, 2002) cited in Karpouzi (2005).

$$BMR = 1.775 \cdot m^{0.768} \quad (J.2)$$

$$FMR = 21.33 \cdot m^{0.626} \quad (J.3)$$

Where Basal and Field Metabolic Rates are given in $kJ \cdot d^{-1}$ and m=mass of the bird in grams. These metabolic rates were then applied to the number of breeding and non breeding days (table J.3) to give a yearly average of metabolic rates given in Karpouzi (2005). Yearly energy required was divided by average energy of all prey items weighted by proportion of diet to give a yearly weight. The calculated consumption rates were generally too high for the model and were decreased to balance the model.

Table J.3: Number of breeding and non-breeding days per year. Q/B values were calculated using equations J.2 and J.3. Data for number of breeding, non-breeding days per year, and weight from Karpouzi (2005).

Species	Non-breeding days	Breeding days	Calculated Q/B (y^{-1})	Model Q/B (y^{-1})	Weight (Kg)	P/B (y^{-1})
Emperor Penguins	91	274	33.69	28.69	30	0.15
Gentoo Penguins	280	85	31.65	29	6	0.2*
Chinstrap Penguins	257	108	38.95	34	4.5	0.3*
Macaroni Penguin	246	119	35.12	25	4.5	0.3
Adelie Penguins	257	108	38.64	30	4.75	0.29
* P/B values were increased for gentoo and chinstrap to account for immigration.						

Emperor Penguins

(*Aptenodytes forsteri*) Emperor penguins are the largest seabirds in the Antarctic, weighing up to 40kg (Kirkwood and Robertson, 1997), and have a circumpolar distribution. Adult female penguins must fast while laying their eggs, and then they have a short amount of time to replenish energy stores before returning to breeding sites to feed newly hatched chicks and then fast once more. Adult males take over responsibility of caring for the unhatched egg, and also must live off energy reserves during this time. Therefore availability of food resources is important to emperor penguins, as both male and female adults require sufficient reserves to survive the winter. Emperor penguin biomass was assumed to be the lowest of all penguin biomasses as they tend to be located on the continent, and was estimated to be roughly 10% of adielie penguin numbers (Ainley et al., 1994) or $0.0013\text{t}\cdot\text{km}^{-2}$, but was increased to $0.005\text{t}\cdot\text{km}^{-2}$ to balance the model.

Cephalopods and fish are important contributors to the diets of emperor penguins. Cephalopod contributions can range from 3-99% of the diet, with fish ranging from 38-97%, depending on season and location around Antarctica (Klages, 1989; Kirkwood and Robertson, 1997; Cherel and Kooyman, 1998). *P. antarcticum* was the most prevalent fish in the diet for all locations. Amphipods were noted to increase frequency in the diet in the spring, with benthic prey being rare year round. Krill also fluctuated in the diet, from 70% of the winter diet in female penguins to 25% of the late summer diet (Green, 1986; Klages, 1989; Putz, 1995). The diet was set to 22% cephalopods, 1% other icefish, 3% Large notothenioids, 3% small notothenioids, 20% *P. antarcticum*, 0.1% arthropod crustaceans, 29.9% adult krill, and 21% sub-adult krill (Green, 1986; Klages, 1989; Putz, 1995; Kirkwood and Robertson, 1997; Cherel and Kooyman, 1998).

Gentoo Penguins

(*Pygoscelis papua*) Gentoo penguins are deep diving, inshore feeding penguins which require large amounts of food near their colonies in order to feed their young (Trivelpiece et al., 1987). During the breeding season gen-

too penguins do not fast, however their ability to make deeper dives than adelie and chinstrap penguins allows them to utilize prey species found in deeper water. Of the global population of 298,000 breeding pairs, 30% were found at South Georgia, and 15% were found within the pack ice region (Trivelpiece et al., 1987). While the Antarctic Peninsula is a smaller population compared to colonies on South Georgia, it was assumed 10% or 29,800 pairs were in the model area leading to a biomass of $0.0005\text{t}\cdot\text{km}^{-2}$. However this had to be increased to $0.0065\text{t}\cdot\text{km}^{-2}$ to balance the model. Although this biomass is relatively high, even compared to numbers at South Georgia, a higher biomass was necessary to account for the predation mortality primarily from killer whales and leopard seals.

As gentoos have increased in abundance at a number of locations on the peninsula (PALMER station on Anvers Island, and Cierva point on Signey Island), a biomass accumulation term was included in the model to account for migration into the region (Quintana et al., 2000; Fraser, 2006). One population at Cierva point on the peninsula has increased an average of 5.7% per year from 1991-1996 (Quintana and Cirelli, 2000), while the population at PALMER station has increased nearly 50 fold from 1991 to 1996 (Fraser, 2006). While data from PALMER station is not believed to be representative of the entire model area, a biomass accumulation of 5.7% a year was incorporated into the model. The production was increased from 0.2 to 0.22y^{-1} to account for the biomass accumulation.

The diet is dominated by fish (primarily *N. rossii*, *N. neglecta*, *C. gunnari*, with some myctophids), krill; contributing on average 50% of the diet, and cephalopods with a few amphipods (Volkman et al., 1980; Croxall et al., 1988; Coria et al., 2000; Clausen and Putz, 2003; Lescroel et al., 2004; Clausen et al., 2005). The diet was set to 32% cephalopods, 1% other icefish, 4% large notothenioids, 4% small notothenioids, 1% deep demersals large, 3% deep demersals small, 1% *C. gunnari*, 1% *P. antarcticum*, 8% *N. gibberifrons*, 2% salps, 2% urochordata, 1% porifera, 2% hemichordata, 1.5% brachiopoda, 1.5% bryozoa, 3% cnidarians, 1% crustaceans, 1% worms, 23% adult krill, 2% sub-adult krill, and 5% macro-zooplankton.

Chinstrap Penguins

(*Pygoscelis antarctica*) Chinstrap penguins are the second most abundant penguin species in the world, with the majority of the population in the Scotia Sea region (Knox, 1994; MacDonald et al., 2002). Range has expanded onto the Antarctic Peninsula with some colonies increasing 6-10% per year or even higher (Fraser et al., 1992). Estimates from the Weddell Sea range from 0.007 to $0.003\text{t}\cdot\text{km}^{-2}$ for areas with ice and without (Van Franeker et al., 1997). The biomass was assumed to be similar to the Weddell Sea and was set to a mid-range value of $0.0053\text{t}\cdot\text{km}^{-2}$. Trends from different islands in the model area identify increases in abundance from the 1950s to the 1980s with fluctuating populations up until the 2000s; of the three study sites, one population increased, one decreased, and one fluctuated from 1980-2000 (Croxall et al., 2002). However, long term data provided from PALMER station (figure J.1) was used in model fitting, as it was the only available data.

A biomass accumulation of 10% per year was incorporated to account for chinstrap penguins moving from other areas onto the peninsula. To account for the biomass accumulation, the P/B ratio was increased from 0.3 to 0.33y^{-1} . Chinstrap penguins are believed to feed exclusively on krill during the breeding season, adjusting the diving depth to coincide with the depth where krill are present (Volkman et al., 1980; Bengtson et al., 1993; Takahashi et al., 2003). Fish, cephalopods, and various benthic species have also been found in the diet, with fish increasing in frequency in areas where adeliae and chinstrap penguins overlap in distribution. The increase of fish in the chinstrap diet is thought to be caused by increased competition for krill (Lynnes et al., 2004). The diet was set to 38% cephalopods, 1% other icefish, 3% large notothenioids, 1% small notothenioids, 1% deep demersals large, 3% deep demersals small, 1% *C. gunnari*, 1% *P. antarcticum*, 4% *N. gibberifrons*, 2% salps, 2% urochordata, 2% porifera, 2% hemichordata, 1.5% brachiopoda, 1.5% bryozoa, 3% cnidarians, 1% crustaceans, 2% worms, 23% adult krill, 2% sub-adult krill, and 5% macro-zooplankton (Volkman et al., 1980; Bengtson et al., 1993; Takahashi et al., 2003; Lynnes et al., 2004).

Macaroni Penguin

(*Eudyptes chrysolophus*) Although macaroni penguins are believed to be the most abundant penguin species in the world (Green et al., 1998), they are considered less abundant than other penguins at the peninsula, contributing less than 1% of the total bird biomass in the Scotia arc-Weddell Sea region (Ainley et al., 1994). Based on total penguin abundance (Van Franeker et al., 1997), average weight (Davis et al., 1989), and distribution of individual penguin species (Whitehouse and Viet, 1994), 1% of total bird biomass, including flying birds would be $0.0008\text{t}\cdot\text{km}^{-2}$, however this was too low for the model, and the biomass was increased to $0.0135\text{t}\cdot\text{km}^{-2}$, or nearly 15% of the biomass of other bird species.

Fish in the diet consists primarily of myctophids, icefish, and notothenioids, which ranges from a small contribution up to half of the diet depending on location (Croxall et al., 1988; Davis et al., 1989; Klages, 1989; Green et al., 1998). Krill is an important prey item during chick rearing which can contribute up to 95% of the total diet. Amphipods and mysidaceans were also present in the diet along with cephalopods (Klages, 1989). The yearly average diet was set to 11% cephalopods, 1.5% other icefish, 5% large notothenioids, 2% small notothenioids, 0.5% deep demersals small, 2% myctophids, 1% other pelagics, 2% *C. gunnari*, 1% *P. antarcticum*, 2% *N. gibberifrons*, 3% crustaceans, 35% adult krill, and 34% sub-adult krill (Croxall et al., 1988; Davis et al., 1989; Klages, 1989; Green et al., 1998).

Adelie Penguins

(*Pygoscelis adeliae*) Adelie penguins are the most abundant penguins over the entire peninsula with estimates ranging from $3.5\text{ animals}\cdot\text{km}^{-2}$ for in-shore areas to less than $1\text{ animal}\cdot\text{km}^{-2}$ for offshore areas (Whitehouse and Viet, 1994). Estimates of 625,800 penguins over three of the Shetland Islands indicate high densities at centralized locations (Trivelpiece et al., 1987). An average of $2.84\text{ animals}\cdot\text{km}^{-2}$ yielded a biomass of $0.016\text{t}\cdot\text{km}^{-2}$, however this was too low and considering estimates from the Shetland Islands, the biomass was increased to $0.034\text{t}\cdot\text{km}^{-2}$ to balance the model. Densities in

the Weddell Sea reach $8 \text{ animals} \cdot \text{km}^{-2}$ on sea ice (Van Franeker et al., 1997), a higher density than noted at the peninsula even though there are believed to be more adelic penguins in the peninsula region.

Fish, cephalopods and krill were the most important prey items to adelic penguins, with krill ranging up to 100% of the diet during breeding season (Volkman et al., 1980). Of the fish prey items *P. antarcticum* was the most prevalent. Amphipods have been noted as a minor contributor to the diet (Green and Johnstone, 1988; Kent et al., 1997; Kerry et al., 1997; Ainley et al., 2003; Efran and Pitcher, 2005). Diet composition was set to 2% cephalopods, 0.3% shallow demersals, 0.5% myctophids, 1% other pelagics, 4% *P. antarcticum*, 8% molluscs, 6% crustaceans, 66.2% adult krill, 10% juvenile krill, and 2% macro-zooplankton (Volkman et al., 1980; Green and Johnstone, 1988; Kent et al., 1997; Kerry et al., 1997; Ainley et al., 2003; Efran and Pitcher, 2005).

Flying birds

The functional group for flying birds contains all species known to inhabit the Antarctic Peninsula either part time or full time based on a global database (Karpouzi, 2005). This includes the following species: southern giant fulmar or southern giant petrel (*Macronectes gigcualoides*), Antarctic petrel (*Thalassoica antarctica*), Snow Petrel (*Pagodroma nivea*), Dominican Gull (*Larus dominicanus*), Grey headed Albatross (*Diomedea chrysostoma*), Light-mantled Sooty Albatross (*Phoebastria palpebrata*), Cape Petrel (*Daption capense*), Blue Petrel (*Halobaena caerulea*), Antarctic Prion (*Pachyptila vittata*), Kerguelen Petrel (*Lugensa brevirostris*), Diving Petrel (*Pelecanoides urinatrix*), Wandering Albatross (*Diomedea exulans*), Black-Browed Albatross (*Diomedea melanophrys*), White chinned petrel (*Procellaria aequinoctialis*), Sooty Shearwater (*Puffinus griseus*), Fairy Prion (*Pachyptila turtur*), Soft-Plumaged Petrel (*Pterodroma mollis*), Black-Bellied Storm Petrel (*Fregetta tropica*), Wilson's Storm Petrel (*Oceanites oceanicus*), American Shearbill (*Chionis alba*), Brown Skua or subantarctic skua (*Catharacta skua*), South Polar Skua (*Catharacta maccormicki*), Antarc-

tic Tern (*Sterna vitatta*), Arctic Tern (*Sterna paradisaea*), Southern Giant Petrel (*Macronectes giganteus*), Blue-eyed Cormorant or blue eyed shag (*Phalacrocorax atriceps*), Southern Black-backed Gull (*Larus dominicanus*), Yellow-billed Sheathbill (*Chionis alba*), Grey-headed Albatross (*Diomedea chrysostoma*).

Van Franeker et al. (1997) provided a biomass for 15 species in the Weddell Sea region of $0.087 \text{ t cot km}^{-2}$, while Whitehouse and Viet (1994) identified the biomass of 21 species at the Antarctic Peninsula to be $0.199 \text{ t cot km}^{-2}$. The latter value was used for the model. Consumption was calculated using an average daily food intake (DFI) value provided by Karpouzi (2005) and comparing it to the energetic value of the prey items in the diet. This provided a Q/B value of 14.88 y^{-1} . The P/B ratio was estimated by the model using an EE of 0.95. The diet of flying birds is highly varied among species including predation on other birds and penguins. Diet for this group was set to: 0.1% adelic penguins, 2.1% flying birds, 21.6% cephalopods, 1% other icefish, 0.1% large notothenioids, 2% small notothenioids, 2% myctophids, 1.6% other pelagics, 1.8% *P. antarcticum*, 0.1% *N. gibberifrons*, 3.2% mollusca, 5% salps, 0.5% cnidarians, 7% crustaceans, 23.4% adult krill, 23.5% sub-adult krill, and 5% copepods (Pakhomov et al., 2002; Karpouzi, 2005).

Cephalopods

Species of this group include all known cephalopods which have been found in the model area: *Alluroteuthis antarcticus*, *Bathyteuthis abyssicola*, *Galioteuthis glacialis*, *Mesonychoteuthis hamiltoni*, *Moroteuthis knipovitchi*, and *Psychroteuthis glacialis* (Xavier et al., 1999), and based on stomach contents of predators (Daneri et al., 2000). The biomass of all cephalopods in the area set to $2.49 \text{ t cot km}^{-2}$ based on estimates from Jackson et al. (2002). The P/B and Q/B were based on values used for cephalopods in the Kerguelen Islands model (Jarre-Teichmann et al., 1997; Pruvost et al., 2005). P/B was set to 0.95 year⁻¹ based on values of 0.6 and 1 y^{-1} for small and large cephalopods, respectively. Q/B was initially set to 2.5 y^{-1} considering values of 2 and 3 y^{-1} for large and small cephalopods; however this value was

too high and was lowered to $2y^{-1}$ to balance the model.

The diet of cephalopods was set to 1% cephalopods, 0.1% other icefish, 0.05% toothfish, 0.1% large notothenioids, 0.5% small notothenioids, 1% myctophids, 1% other pelagics, 7.5% *P. antarcticum*, 1% mollusca, 4.25% salps, 0.4% urochordata, 0.5% cnidarians, 5% crustaceans, 3.25% arthropod other, 4.9% worms, 11.8% adult krill, 33% juvenile krill, 13.1% macro-zooplankton, and 8% micro-zooplankton (Hureau, 1994; Lu and Williams, 1994; Kozlov, 1995; Rodhouse and Nigmatullin, 1996).

Fish

Fish groupings were based on familial characteristics and feeding preferences. Those species known to be important prey items to a variety of predators were given their own functional grouping. Factors taken into account for groupings were size, depth, family, feeding strategy, and habitat preference (Daniels and Lipps, 1989; Knox, 1994; Barrera-Oro et al., 2000; Kock et al., 2000).

Biomass for all fish groups was estimated from surveys, relative abundance data, presence-absence data, known ranges for each species, and then broken down by species to give each group biomass. In general species were reported as a percentage of total catch or a biomass was given for individual species (Kock, 1992; Knox, 1994; Frolkina et al., 1998; Kock, 1998; Arana and Vega, 1999; Jones et al., 2000; Kock et al., 2000, 2004; Kock and Jones, 2005; Froese and Pauley, 2008). It is likely that biomass estimates from these surveys will underestimate the fish biomass, and in some cases biomass was increased to balance the model.

Total mortality was set to the sum of fishing mortality and natural mortality. Fishing mortality occurs to all functional groups except the demersal fish, however the fishing mortality caused within the first year was set to be negligible (see fishery section). Therefore, natural mortality (M) was assumed to equal the Production/Biomass ratio, and was calculated using 2 methods. The first equation J.4 (Pauly, 1980; Froese and Pauley, 2008) and

equation J.5 (Jensen, 1997) with the results in table J.4.

$$M = 10^{0.566 - 0.718 \cdot \log L_{\infty} + 0.02 \cdot T} \quad (\text{J.4})$$

$$M = 1.5k \quad (\text{J.5})$$

where L_{∞} is the maximum length a fish would grow to in a population and T represents temperature in degrees Celsius, which was set to 0.5°C as a yearly average (Dierssen et al., 2002). Max length values were taken from fishbase and published literature (Daniels, 1982; FAO, 1985a,b; Kock, 1992; Frolkina et al., 1998; Arana and Vega, 1999; Kock et al., 2000, 2004; Kock and Jones, 2005; Froese and Pauley, 2008). Although equation J.4 is based on 175 fish stocks, it underestimates the mortality for polar species (Pauly, 1980), so a second equation (eq. J.5) for mortality was used in comparison; where k is the growth coefficient. If mortality rates could be calculated for all or most species in the functional group then the average mortality rate was taken. If the value was known for only one species, than that value was used for the functional group.

Consumption rates were calculated using equation J.6 (Palomares and Pauly, 1998);

$$\log \frac{Q}{B} = 7.964 - 0.204 \cdot \log W_{\infty} - 1.965T' + 0.532h + 0.398d \quad (\text{J.6})$$

Where W_{∞} is the weight a fish would reach if it grew to L_{∞} , T is the mean environmental temperature ($1000 / (C + 273.15)$) with C representing temperature in degrees Celsius, A is the aspect ratio of the caudal fin (with the default value= 1.32), h and d represent variables for feeding types; $h=1$ if the fish is a herbivore, $h=0$ if it consumes other food types, $d=1$ if the fish is a detritivore, $d=0$ if the fish consumes other food types. Temperature was set to 0.5°C based on winter and summer temperatures (Dierssen et al., 2002). Pakhomov (unpublished data) indicate daily consumption rates of demersal fish ranging from 0.5-4% of body weight, leading to annual Q/B ratios from $1.82\text{-}14.6\text{y}^{-1}$. This indicates equations from Palomares and Pauly (1998) may be underestimating consumption of polar species.

Table J.4: Calculated mortality and consumption values for fish groups. Biomass (B) is presented from surveys in $t \cdot km^{-2}$. Mortality (M), production to biomass ratio (P/B) and consumption to biomass (Q/B) are presented as a yearly rate (y^{-1})

	Group	B	Species	K	Reference	M1‡	M†	Model P/B	Q/B*	Model Q/B
20	Other Icefish	0.337	Family value	0.273	Froese and Pauley (2008)	0.409	0.32	0.38	1.57	1.57
			<i>P. georgianus</i>	0.32	Froese and Pauley (2008)	0.48				
21	Toothfish	0.047	<i>D. elegiodes</i>	0.102	Horn (2002)	0.152	0.14	0.165	0.7	0.77
			<i>D. mawsoni</i>	0.099	Horn (2002)	0.148				
22	Lg. Nototheniidae	0.59	Family value	0.133	Froese and Pauley (2008)	0.19	0.19	0.37	2.76	1.95
			<i>N. coriiceps</i>	0.098	Coggan (1997)	0.147				
23	Sm. Nototheniidae	0.341	Family value	0.364	Froese and Pauley (2008)	0.546	0.43	0.65	2.53	2.2
24	Shallow Demersals	0.031	<i>H. antarcticus</i>	0.14	Daniels (1983)	0.21	0.37	0.75	4.65	4.125
			<i>H. antarcticus</i>	0.25	Daniels (1983)	0.375				
25	Deep Demersals Lg.	0.042	<i>P. brachycephalum</i>	0.31	Froese and Pauley (2008)	0.465	0.18	0.29	2	2.18
			<i>O. amberensi</i>	0.31	Froese and Pauley (2008)	0.465				
26	Deep Demersals Sm.	0.08	p. brevipes		Froese and Pauley (2008)		0.4	0.65	2.7	2.7
27	Myctophids	0.185	Family value	0.43	Froese and Pauley (2008)	0.64	0.53	1.35	3.4	3.73
28	Other Pelagics	0.49	<i>A. pharao</i>	0.5	Froese and Pauley (2008)	0.75	0.22	0.55	1.83	2.02
			<i>B. antarcticus</i>	0.14	Froese and Pauley (2008)	0.21				
29	<i>C. gunnari</i>	0.29	<i>C. gunnari</i>	0.141	Froese and Pauley (2008)	0.212	0.22	0.48	2.4	1.8
30	<i>P. antarcticum</i>	1.25	<i>P. antarcticum</i>	0.093	Froese and Pauley (2008)	0.14	0.19	1.1	1.1	3.55
31	<i>N. gibberifrons</i>	0.81	<i>N. gibberifrons</i>	0.104	Froese and Pauley (2008)	0.156	0.11	0.41	1.4	1.55

†Natural mortality calculated using eq. J.4 (Pauly, 1980)

‡Natural mortality calculated using eq. J.5 (Jensen, 1997)

*Consumption calculated using eq. J.6 (Palomares and Pauly, 1998)

Other Icefish

This group represents all icefish species with the exception of *C. gunnari* which is an important prey item for many species, and thus was given its own functional group. All other icefish in the area consist of; *Chaenocephalus aceratus*, *Chaenodraco wilsoni*, *Chionodraco rastrospinosus*, *Cryodraco antarcticus*, *Neopagetopsis ionah*, *Pagetopsis macropterus*, *Chionobathyscus dewitti* and *Pseudochaenichthys georgianus*. Diet was set to 1.5% cephalopods, 0.5% other icefish, 0.05% toothfish, 3.05% large notothenioids, 3.5% small notothenioids, 0.4% deep demersals large, 1.5% deep demersals small, 4% *C. gunnari*, 5% *P. antarcticum*, 18% *N. gibbifrons*, 2% mollusca, 3% salps, 2.5% cnidarians, 3% crustaceans, 0.5% arthropods other, 2% worms, 18.5% adult krill, 19% sub-adult krill, 7% macro-zooplankton, 3% micro-zooplankton, and 2% copepods (Pakhomov et al., 2002; Flores et al., 2004; Kock et al., 2004).

Toothfish

The toothfish group included two species: *Dissostichus eleginoides* and *Dissostichus mawsoni*. P/B biomass was increased slightly beyond the calculated values to 0.165y^{-1} in order to balance the model. The diet was set to: 17.4% cephalopods, 20% other icefish, 6% large notothenioids, 15% small notothenioids, 0.5% deep demersals large, 1% deep demersals small, 2% myctophids, 1% other pelagics, 5% *C. gunnari*, 4% *P. antarcticum*, 8% *N. gibbifrons*, 1.1% salps, 0.5% cnidarians, 8.5% crustaceans, 1% other arthropods, 1% worms, 4% adult krill, and 4% sub-adult krill (Garcia de la Rosa et al., 1997; Arana and Vega, 1999).

Large Notothenioids

Large Nototheniidae were classified as fish in the family Nototheniidae with an average length over 30 cm. This included *Notothenia coriiceps*, *Notothenia (Notothenia) neglecta*, *Notothenia rossii*, *Pagothenia (Trematomus) hansonii* and *Notothenia squamifrons*. The P/B ratio was increased

to 0.37y^{-1} to balance the model, and the diet was set to: 0.5% large notothenioids, 1.5% small notothenioids, 0.1% shallow demersals, 0.1% deep demersals large, 0.25% deep demersals small, 2% myctophids, 2% other pelagic, 0.5% *C. gunnari*, 2% *P. antarcticum*, 0.5% *N. gibberifrons*, 4% mollusca, 3% salps, 0.25% cnidarians, 28.4% crustaceans, 2% other arthropods, 7% worms, 16.8% adult krill, 16% juvenile, 0.1% larval krill and krill embryos together, 3% Macro-zooplankton, 5% Ice algae, and 5% other phytoplankton (Casaux et al., 1990; Kozlov, 1995; Pakhomov et al., 2002).

Small Notothenioids

Small notothenioids were classified as fish from the family Notothenoidea with an average length less than 30 cm. This included *Cryothenia peninsulae*, *Notothenia (Lepidonotothen) larseni*, *Notothenia (Lepidonotothen) nudifrons*, *Trematomis loennbergi*, *Pagothenia (Trematomus) bernacchii*, *Trematomus newnesi*, *Trematomus scotti*, *Trematomus eulepidotus*, and *Trematonius centronotus*. The diet for these species was set to: 11% mollusca, 2% salps, 1% urochordates, 1% cnidarians, 35% crustaceans, 0.1% other arthropods, 19% worms, 0.2% Echinoidea, 0.2% Crinoidea, 0.2% Ophiuroidea, 0.2% Asteroidea, 1.1% Holothuroidea, 10% Adult krill, 10% juvenile krill, 0.1% larval krill, 3.9% Macro-zooplankton, 2% Micro-zooplankton, and 3% copepods (Casaux et al., 1990; Vacchi et al., 1994; Pakhomov et al., 2002).

Shallow Demersals

Shallow demersals were classified as demersal fish typically found in depth ranges of 0-200m. This included *Artedidraco skottsbergi*, *Harpagifer antarcticus*, and *Harpagifer bispinis*. The P/B ratio was increased to 0.75y^{-1} to balance the model, and diet was set to: 7.5% Mollusks, 2% salps, 75% crustaceans, 2% other arthropods, 4.5% worms, 7% adult krill, and 2% sub-adult krill (Duarte and Moreno, 1981; Casaux, 1998; Pakhomov et al., 2002).

Large Deep Demersals

This group was characterized by an average depth of 200 m or deeper, and an average size of 30 cm or larger. This included *Parachaenichthys charcoti*, *Gymnodraco acuticeps*, *Mancopsetta maculata*, *Muraenolepis microps*, *Pachycara brachycephalum*, *Paradiplospinus antarcticus*, *Ophthalmolycus amberensi*, *Bathyraja eatonii*, *Bathyraja maccaini*, and *Bathyraja sp2*. Diet was set to: 5% cephalopods, 3.5% other icefish, 0.5% toothfish, 4% large notothenioids, 4% small notothenioids, 2% shallow demersals, 7% deep demersals small, 2% *C. gunnari*, 7% *P. antarcticum*, 2% *N. gibbifrons*, 15% mollusca, 1% salps, 2% urochordates, 0.5% hemichordates, 2% cnidarians, 7% crustaceans, 0.5% other arthropods, 4.5% worms, 12% adult krill, 9% juvenile krill, 1% larval krill and krill embryo, 4% macro-zooplankton, 2% micro-zooplankton, and 2.5% other phytoplankton.

Small Deep Demersals

Small deep demersals were categorized by having an average depth of 200m or greater, and an average size of 30 cm or less. This included *Pogonophryne marmorata*, *Prionodraco evansii*, *Psilodraco breviceps*, and *Paraliparis antarcticus*. The diet for this group was set to: 4% cephalopods, 5% other icefish, 7% small notothenioids, 0.5% shallow demersals, 1% deep demersals small, 4% myctophids, 4% other pelagic, 8% *P. antarcticum*, 15% mollusca, 2% salps, 0.5% urochordata, 0.5% bryozoa, 0.1% cnidarians, 20.5% crustaceans, 0.5% other arthropods, 8% worms, 8.4% adult krill, 4.9% juvenile krill, 0.5% larval krill, 0.1% krill embryo, 5% macro-zooplankton, and 0.5% micro-zooplankton.

Myctophids

Fish belonging to the family Myctophidae were included in this group, which carry considerable vertical migration to utilize food and resources in the epipelagic zone. For this region this includes: *Electrona antarctica*, *Gymnoscopelus braueri*, *Gymnoscopelus nicholsi*, *Gymnoscopelus opisthopterus*, and *Protomyctophum bolini*. Both P/B and Q/B ratios were increased to 1.35y^{-1}

and 3.73y^{-1} respectively to balance the model. The diet was set to: 25% mollusca, 2% salps, 23% crustaceans, 1% worms, 15% adult krill, 5% juvenile krill, 4% macro-zooplankton, and 25% copepods (Hureau, 1994; Kozlov, 1995; Greely et al., 1999; Pakhomov et al., 2002; Shreeve et al., 2005).

Other Pelagics

Other pelagic included all other species inhabiting the pelagic zone not in the family *Myctophidae*: *Anotopterus pharaoh*, *Bathylagus antarcticus*, *Lampris immaculatus*, *Paradiplospinus gracilis*, and *Paradiplospinus antarcticus*. The diet was set to: 25% cephalopods, 1% other icefish, 1.5% small notothenioids, 0.1% deep demersals large, 0.1% deep demersals small, 3% myctophids, 2% other pelagics, 10% *P. antarcticum*, 4% mollusks, 5% salps, 0.5% brachiopods, 0.5% bryozoans, 1.5% cnidarians, 5% crustaceans, 2% worms, 16% adult krill, 16.9% juvenile krill, 4% macro-zooplankton, and 1.9% micro-zooplankton (Jackson et al., 2000; Pakhomov et al., 2002).

Champsoccephalus gunnari

For *C. gunnari*, the P/B ratio was increased to 0.48y^{-1} , and the Q/B ratio was lowered to 1.8y^{-1} to balance the model. The diet was set to: 1% myctophids, 3% salps, 1% arthropod crustaceans, 1.5% worms, 47% adult krill, 44.5% juvenile krill, 1% macro-zooplankton, 1% micro-zooplankton (Kock and Everson, 2003; Flores et al., 2004).

Pleuragramma antarcticum

The P/B and Q/B ratios were increased to 1.1y^{-1} and 3.55y^{-1} respectively to balance the model. The diet for this group was set to: 0.1% other icefish, 0.1% small notothenioids, 0.1% deep demersals small, 1% other pelagic, 0.5% *P. antarcticum*, 1% *N. gibberifrons*, 13.3% mollusks, 1% salps, 0.1% cnidarians, 10% crustaceans, 1% other arthropods, 3% worms, 4% adult krill, 35% juvenile krill, 8% macro-zooplankton, 3.8% micro-zooplankton, and 18% copepods (Eastman, 1985; Hubold, 1985).

Notothenia gibberifrons

The P/B ratio for *N. gibberifrons* was increased to 0.41y^{-1} to balance the model while the diet was set to: 2% mollusks, 1% salps, 1% urochordates, 1% cnidarians, 38% crustaceans, 1% other arthropods, 12% worms, 1% holothuroideans, 12% adult krill, 14% juvenile krill, 0.1% larval krill, 2.9% macro-zooplankton, 1% micro-zooplankton, 1% cryptophytes, 1% copepods, 1% diatoms, 5% ice algae, and 5% other phytoplankton (Casaux et al., 1990, 2003).

Invertebrates

Grouping for invertebrates were based on previous models of Antarctic peninsula and Weddell Sea regions (Jarre-Teichmann et al., 1997; Efran and Pitcher, 2005) taking into account invertebrate groups important to the diets of top predators. Species with low biomass or those not significantly contributing to the diet of higher level predators were generally combined to make one larger species group. Likewise, species which were quite important to higher predators were split into one or more groups.

Table J.5: Benthic habitat by depth range for the Antarctic Peninsula

Depth	Percentage of total Habitat
<10m	1.66
11-50m	3.94
51-100m	3.89
101-200m	6.59
201-1000m	33.99
>1000m	49.94

Jazdzewski et al. (1986) provided benthic surveys from 18 stations ranging from 15-250 meters in depth at King George Island in the South Shetlands for the 1980s. Saiz-Salinas et al. (1998) sampled 73 stations ranging from 32-421 meters between 1994-1995 near Livingston Island in the South Shetlands. Piepenburg et al. (2002) re-sampled King George Island in 1998 taking transects 130-2000 meters. These three surveys provided biomass estimates for each of the functional groups in the model, at various depths.

The final biomass was based on the average biomass for each depth range compared to percentage of habitat for each depth (table J.5), as provided by the GIS basemap function in Ecopath version 5 (Christensen et al., 2005).

Invertebrate groups where published production values could not be found, were calculated using equation J.7 (Brey, 1999) where B is the biomass ($\text{g DM}\cdot\text{m}^{-2}$), M is maximum individual body mass (g DM), T is the surface temperature of the water ($^{\circ}\text{C}$), and D is the depth of water (in meters). Temperature was set to 0.5°C , and depth was taken as the average depth the functional group was found in surveys. Individual body mass was taken from Saiz-Salinas et al. (1998) and converted to dry mass (DM) using values in Brey (2004, 2009).

$$\log(P) = 0.240 + 0.960 \cdot \log(B) - 0.210 \cdot \log(M) + 0.030 \cdot T - 0.160 \cdot \log(D + 1) \quad (\text{J.7})$$

Consumption rates were based on published literature as shown (table J.6), and diet information was provided on a per species basis. However, diet information was generally provided for summer months, when most research is conducted in the Antarctic. It was formerly believed that feeding ceases in the winter months, however recent studies (Barnes and Clarke, 1995; Peck et al., 2005) identify feeding throughout most of the winter. It has been suggested that ice scour, which directly damages benthic communities, may also help re-suspend particles in the sediment making them available for suspension feeders (Orejas et al., 2000). Antarctic brachiopods which take advantage of the abundant summer food supply, however in the winter they rely on re-suspended benthic material (Peck et al., 2005). It is likely other benthic species also rely on this strategy for feeding during the winter months. Therefore, annual diets have been adjusted to incorporate re-suspension of detritus as a food source.

Molluscs

Surveys revealed the biomass and abundance of this group was dominated by bivalves. Other taxonomic groups included Gastropods, namely Opisthobranchs (sea slugs) and Prosobranchs (snails), and in smaller numbers

Scaphopods (tusk shells). Solenogastres (Aplacophors or shell-less mollusks) were also present, but not a substantial part of this functional group. While the majority of bivalves were assumed to be filter feeders, other species of molluscs have been reported to consume different types of worms (Jarre-Teichmann et al., 1997). The diet for this group was heavily weighted to account for large amounts of bivalves and was set to: 6% worms, 1% macro-zooplankton, 2% micro-zooplankton, 2% cryptophytes, 1% copepods, 5% diatoms, 5% ice algae, 5% other phytoplankton, and 73% detritus.

Urochordata

This group was primarily comprised of ascidians or sea squirts, and includes all urochordates except salps. As filter feeders (Jarre-Teichmann et al., 1997) the diet was set to 10% micro-zooplankton, 15% cryptophytes, 3% copepods, 15% diatoms, 15% ice algae, 30% other phytoplankton, and 12% detritus.

Porifera

Based on surveys sponges are quite abundant at the peninsula, and they have been shown to be important to the diets of various echinoderms. As filter feeders, the diet has been noted to consist primarily of detritus (Jarre-Teichmann et al., 1997). The diet was set to 2% cryptophytes, 2% diatoms, 2% ice algae, 2% other phytoplankton, and 92% detritus.

Hemichordata

Acorn worms (class Enteropneusta) were the only representatives found in surveys. In the Weddell Sea they are assumed to be complete detritivores (Jarre-Teichmann et al., 1997), so the diet was set to 100% detritus for the peninsula as well.

Brachiopoda

Brachiopods, or lampshells were not shown to be a significant contribution to invertebrate biomass through surveys. They have the ability to switch

from pelagic feeding, taking advantage of the summer phytoplankton, to benthic food sources such as the re-suspended particles (Peck et al., 2005). The diet was set to, 10% micro-zooplankton, 5% cryptophytes, 5% copepods, 5% diatoms, 5% ice algae, 20% other phytoplankton, and 50% detritus.

Bryozoa

Bryozoans were found in most of the survey samples taken from the region. As filter feeders, they generally consume smaller particles (Barnes and Clarke, 1995). The diet was set to 5% micro-zooplankton, 15% cryptophytes, 5% copepods, 15% diatoms, 15% ice algae, 15% other phytoplankton, and 30% detritus.

Cnidarians

The cnidarian group is primarily comprised of sea anemones (anthozoans), sea fans (gorgonians), and hydroids (hydrozoans), but includes all pelagic and sessile stages of reproduction. Hydroids and anthozoans have been shown to consume a variety of foods such as diatoms, invertebrate larvae and eggs, copepods, nematodes, salps, and detritus (Orejas et al., 2001). The diet was set to 10% salps, 5% macro-zooplankton, 20% micro-zooplankton, 10% cryptophytes, 5% copepods, 5% diatoms, 5% ice algae, 10% other phytoplankton, 30% detritus.

Crustaceans

Arthropods were split into three main groups: crustaceans, other arthropods, and krill. The crustacean group represents all crustaceans except krill and includes the following taxa based on survey samples; loricata, ostracoda, leptostraca, cumacea, tanaidacea, isopoda, and amphipoda. Amphipods and isopods had the highest contribution to biomass of this group. In the Arctic amphipods feed primarily on ice algae as juveniles, moving on to calanoid copepods as they mature (Scott et al., 2001). The diet for crustaceans was set to; 1% porifera, 0.5% bryozoa, 0.5% cnidarians, 1% crustacean, 0.5% arthropod other, 5.5% worms, 3% holothuroidea, 10% macro-

zooplankton, 9% copepods, 10% ice algae, 5% other phytoplankton, and 54% detritus (Jarre-Teichmann et al., 1997; Scott et al., 2001; De Broyer et al., 2003).

Other Arthropods

The remaining arthropods found in sample surveys were pycnogonidia (sea spiders) and acari (arachnids: ticks and mites). The biomass of these remaining arthropods was lower than the crustaceans, and they were separated primarily due to the dietary importance of crustaceans to higher level organisms. The diet for the group was set based on pycnogonida diet information at: 8% mollusks, 1% salps, 5% urochordata, 1% porifera, 1% bryozoa, 1% cnidarians, 5% crustaceans, 1.5% other arthropods, 23% worms, 0.1% echinoidea, 0.1% crinoidea, 0.1% ophiuroidea, 3.1% asteroidea, 12% holothuroidea, 0.5% juvenile krill larvae, 0.2% krill embryo, 5.5% macro-zooplankton, 4% micro-zooplankton, 2.5% copepods, and 25.4% detritus (Child, 1998).

Worms

The worm functional group contains all worms except the hemichordates. Surveys show a variety of flatworms (Turbellaria), ribbon worms (Nemertini), peanut worms (Sipuncula), roundworms (Nematoda), ringed worms (Polychaeta, Oligochaeta, and Hirudinea), and penis worms (Priapulida). As these groups are a combination of filter feeders and detritivores the diet was set to 3% mollusks, 0.6% urochordata, 2.5% porifera, 0.1% bryozoa, 0.2% cnidarians, 0.2% crustaceans, 0.5% other arthropod, 3.9% worms, 1% echinoidea, 0.01% crinoidea, 2.5% ophiuroidea, 0.5% asteroidea, 1.7% holothuroidea, 15% macro-zooplankton, 4.5% micro-zooplankton, 3% diatoms, and 60.5% detritus (FAO, 1985a,b; Brueggman, 1998; Pakhomov et al., 2002).

Echinoderms

Echinoderms were split into family groupings, as they are one of the largest phyla in the study in terms of biomass, and it is believed they are one of the most important groups of animals to transfer energy within the benthos (McClintock et al., 2005).

Echinoidea

Jacob et al. (2003) show the typical food of sea urchins to be sponges and hydroids (cnidarians) with bryozoans and diatoms also contributing to the standard diet. Other studies indicate a more diverse diet including polychaetes, tunicates, diatoms, and algal matter (McClintock, 1994). The diet was set to 1% mollusks, 0.5% urochordata, 5% porifera, 0.05% hemichordata, 0.2% brachiopoda, 0.8% bryozoa, 1% cnidarians, 5% crustaceans, 2% other arthropods, 17.2% worms, 0.1% crinoidea, 1% ophiuroidea, 1% asteroidea, 4% holothuroidea, 0.1% krill embryo, 8% macro-zooplankton, 3% micro-zooplankton, 8% copepods, 2% diatoms, 2% ice algae, 5% other phytoplankton, and 33.1% detritus (Jacob et al., 2003).

Crinoidea

Crinoids (sea feathers) are the least abundant of all echinoderms, and are known to be filter feeders. The diet was set to 12.5% bryozoa, 4% arthropod crustaceans, 12.5% worms, 2% macro-zooplankton, 2% micro-zooplankton, 1% copepods, and 66% detritus (McClintock, 1994; Jarre-Teichmann et al., 1997).

Ophiuroidea

According to McClintock (1994) brittle stars consume a variety of food such as zooplankton, other brittle stars, detritus, polychaetes, diatoms, gastropods, and copepods. Other studies (Dearborn et al., 1996) show the top five prey groups to be sponges, ophiuroids, bivalves, polychaetes, and crustaceans. The diet for ophiuroids was set to 7% mollusks, 3% porifera, 0.3%

bryozoa, 0.5% cnidarians, 2.5% crustaceans, 10% worms, 5% ophiuroidea, 3.2% macro-zooplankton, 5.9% micro-zooplankton, 3.2% cryptophytes, 1% copepods, 2% diatoms, 2% ice algae, 2% other phytoplankton, and 52.4% detritus.

Asteroidea

The diet of asteroids has been shown to be quite diverse, including detritus, sponges, necrotic tissue, algae, zooplankton, fecal matter, and predation on other invertebrates (McClintock, 1994; Jarre-Teichmann et al., 1997). The diet for this group was set to; 1% mollusks, 1% salps, 1% urochordata, 2% porifera, 1% crustaceans, 5% worms, 5% ophiuroidea, 5% macro-zooplankton, 5% micro-zooplankton, 2% copepods, 2% diatoms, 2% ice algae, 2% other phytoplankton, 66% detritus.

Holothuroidea

Antarctic holothuroideans (sea cucumbers) are known to be suspension feeders (McClintock, 1994; Jarre-Teichmann et al., 1997), therefore the diet was set to 1% diatoms, 1% other phytoplankton, 98% detritus.

Table J.6: Published, calculated, and model mortality (P/B) and consumption (Q/B) rates for invertebrate groups

Model Group	Model P/B	Calc. P/B	Group	Source	Model Pub Q/B	Source
32 Mollusca	0.639	0.309	Mollusca	Brey and Gerdes (1998)	2.556	Estimated by model
		0.778	Bivalve	Brey and Clarke (1993)		
		0.432	Bivalve	Brey and Clarke (1993)		
		0.497	Gastropod	Brey and Clarke (1993)		
		0.305	Benthic Mollusca	Jarre-Teichmann et al. (1997)		
33 Salps	10				33	Estimated by model
34 Urochordata	0.234	0.23	Tunicata	Brey and Gerdes (1998)	1	Jarre-Teichmann et al. (1997)
		0.1	Tunicata	Jarre-Teichmann et al. (1997)		
		0.234	combined‡	Brey (2001)		
35 Porifera	0.159	0.159	Porifera	Brey and Gerdes (1998)	0.795	Efran and Pitcher (2005)
		0.03	Porifera	Jarre-Teichmann et al. (1997)	0.6	
		0.116	combined‡	Brey (2001)		
36 Hemichordata	0.375	0.155	Hemichordata	Brey and Gerdes (1998)	2	Jarre-Teichmann et al. (1997)
		0.3	Hemichordata	Jarre-Teichmann et al. (1997)	2	

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Table J.6 Continued								
Model	Group	Model P/B	Calc. P/B	Group	Source	Model Q/B	Pub Q/B	Source
			0.6	Polychaeta and other worms	Jarre-Teichmann et al. (1997)		4	Efran and Pitcher (2005)
				all worms			4	Jarre-Teichmann et al. (1997)
43	Echinoidea	0.116	0.164	all echinoderms	Brey and Gerdes (1998)	0.464		Estimated by model
			0.116	Echinoidea	Brey and Clarke (1993)			
44	Crinoidea	0.125	0.164	all echinoderms	Brey and Gerdes (1998)			
			0.1	Crinoidea	Jarre-Teichmann et al. (1997)	0.8	1	Jarre-Teichmann et al. (1997)
45	Ophiuroidea	0.45	0.164	all echinoderms	Brey and Gerdes (1998)	1.8		Estimated by model
			0.566	Ophiuroidea	Brey and Clarke (1993)			
			0.173	Ophiuroidea	Jarre-Teichmann et al. (1997)			
46	Asteroidea	0.231	0.164	All echinoderms	Brey and Gerdes (1998)	0.924		Estimated by model
			0.221	Asteroidea	Brey and Clarke (1993)			
			0.164	Asteroidea	Brey and Clarke (1993)			
			0.376	Asteroidea	Brey and Clarke (1993)			
47	Holothuroidea	0.315	0.164	all echinoderms	Brey and Gerdes (1998)			
			0.1	Holothuroidea	Jarre-Teichmann et al. (1997)	1.1	1.1	Jarre-Teichmann et al. (1997)

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Table J.6 Continued						
Model Group	Model Calc. P/B	Group P/B	Source	Model Pub Q/B	Q/B	Source
	0.315	combined‡	Brey (2001)			
†Where P/B values were calculated for various species within the functional group, average value is presented.						
‡P/B was calculated using eq. J.7 (Brey, 2001) with the average value of all species presented.						

Zooplankton

Zooplankton surveys from the Antarctic peninsula and surrounding areas indicate the zooplankton biomass is dominated by krill (*Euphausia superba*) and copepods. Surveys indicating biomass divided the catches into taxonomic groupings generally based on biomass. For the model these survey results were used to delineate proportions of the total zooplankton biomass into the specific functional groups. Salps, krill, and copepods are separated from the rest of the zooplankton due to increased understanding of their roles within the ecosystem, and their importance to the food web.

Calbert et al. (2005) estimated macro-zooplankton biomass ranging from 17-542 $\text{mgC}\cdot\text{m}^{-2}$ while the meso-zooplankton ranged from 55-1741 $\text{mgC}\cdot\text{m}^{-2}$ for samples from the Gerlache Strait, Bransfield Strait, and Bellingshausen Sea for 2002. The meso-zooplankton samples included krill, copepods, and salps so the biomass would be considerably lower when these groups were removed. Estimates from other areas of the Scotia Sea range up to 6150 $\text{mgC}\cdot\text{m}^{-2}$ (roughly 51 $\text{g}\cdot\text{m}^{-2}$ ²¹ from a sample from South Georgia in 1994 sampling primarily meso-zooplankton. While the biomass at South Georgia is high, the Antarctic peninsula is considered a source population for krill, and potentially transports other zooplankton species (Brierley et al., 1999) indicating the total zooplankton biomass could be at least as high as South Georgia.

Salps

The salps group refers specifically to the tunicate *Salpa thompsoni*. Salps graze smaller phytoplankton such as cryptophytes (which are associated with warmer water temperatures and lower salinities), being able to reduce the amount of carbon available to predators by 70% (Moline et al., 2004), thus they were believed to be a trophic dead end in the food web. However research into their ecology indicates they are consumed by some fish and invertebrates (Dubischar et al., 2006). In warmer years salps tend to dominate

²¹Using the conversion $1\text{gC}=8.3$ wet weight for general zooplankton conversion taken from Cushing et al. (1958) as cited in Cauffope and Heymans (2005)

the zooplankton biomass, whereas in cooler years diatoms are more available which increase the transfer of carbon to krill and then further up the food chain. Salps have been shown to remove a majority of primary production later in the summer (march) which may contribute to poor krill larvae biomass as they compete for this food source (Perissinotto and Pakhomov, 1988; Huntley et al., 1989).

Atkinson et al. (2004) estimated the salp abundance at the peninsula to be $33 \text{ salps} \cdot \text{m}^{-2}$ in 1978, with an average abundance of $49.4 \text{ salps} \cdot \text{m}^{-2}$ from 1978-2003. Siegel et al. (2005) showed an average biomass of $12.17 \text{ g} \cdot \text{m}^{-2}$ from 1981-2002 (range $0.76\text{-}75.23 \text{ g} \cdot \text{m}^{-2}$). $12.17 \text{ t} \cdot \text{m}^{-2}$ was used as a starting biomass, but this was too high, so it was lowered to $8 \text{ t} \cdot \text{m}^{-2}$ to balance the model. Pakhomov et al. (2002) noted that although salps have a short pulse of abundance, the P/B of an annual life cycle was likely between 1 and 3 based on studies by other researchers. However, this value was thought to be too low and was increased to 10 y^{-1} ,

Salps are generally filter feeders, whose biomass has been shown to increase in years associated with smaller phytoplankton (Moline et al., 2004; Dubischar et al., 2006). Diets of salps are composed of diatoms and flagellates (von Harbu et al., 2011). Based in this the diet was set to, 10% micro-zooplankton, 30% cryptophytes, 11% copepods, 15% diatoms, 34% other phytoplankton.

Krill

Krill are a central link in the food web, as an important prey item for marine mammals, fish, and birds. In addition they are the only species in the model area to be fished commercially. Due to their importance in the food web, and the fishery operating on the older age classes, multi-stanza groups were created to represent the different life stages of krill.

Multistanza groups are used to provide more detailed information about the life history of a species or species group within the model. Because predation is higher on adult krill, as some species target larger size classes (Lowry et al., 1998). For each multistanza group the mortality (Z) is entered

along with the biomass and consumption for the leading or oldest stanza group (Christensen et al., 2005). Diets for each multi-stanza group can be different and are entered in the diet matrix the same way for other functional groups.

Within the model it is assumed that the species follow a von Bertalanffy growth curve where weight is proportional to length cubed (Christensen et al., 2005), with the growth parameter k used as an input to determining the biomasses of each stanza group. Biomass for the oldest group is entered and internal calculations of survivorship and biomass using the growth parameter K are calculated over monthly time steps to allow a more detailed resolution of age classes. The Von Bertalanffy k parameter has been estimated to be 0.478 for *Euphausia superba* at the Antarctic Peninsula and $k=0.75$ at South Georgia (Siegel, 1987; Reid, 2001). The value of 0.473 was used for the model in order to get a more accurate representation of biomass distribution of stanza groups.

The krill model group representing *Euphausia superba* was broken down into four stanzas: The Krill Embryo stage represents the spawned eggs which sink to the meso- and bathypelagic, hatch and re-ascend as early larvae. Antarctic krill are broadcast spawners, releasing their eggs to sink to into the deep water where there is less predation. During decent eggs rely on the yolk sack for nutrients until about 425-1090m depending on temperature and geographic location (Hofmann et al., 1992). They do not feed during this stage, as they have carbon reserves that can last for roughly 26 days. This represents the Naupli and Metanauplii stages, before the gut and mouthparts have developed (Marr, 1962; Nicol et al., 1995; Arndt and Swadling, 2006). This stanza group ranges from month 0 to 1 month in age. For this group the diet was set to 100% imported, as these groups do not feed within the model, as they live off stored reserves.

The krill Larvae stage is the first feeding stage of krill starting from calyptopis I (CI) where the mouth and guts develop. Phytoplankton is a critical resource for this stage, and timing of the bloom can affect the survival; generally if food is not found within 10-14 days the larvae cannot recover (Ross and Quetin, 1986). These surface dwellers pass through three

stages to become furcilia (where there are 6 stages), the duration of every larval stage being between 8 and 15 days (FAO, 2011). The krill larval stage in the model covers krill ages 1 to 6 months, with the next stage (juveniles) starting at month 7. This stage is somewhat dependent on sea ice, as larval krill located under the sea ice in the autumn and winter show better physiological condition than larvae in open water, and during low food conditions in the water column, larvae feed on ice algae (Meyer et al., 2002, 2009). Prey items for the larval stage include small copepods, protozoans, and autotrophic food sources, however they have the ability to switch to more heterotrophic food sources in the winter (Meyer et al., 2009). The diet for this group was set to 1% micro-zooplankton, 3% cryptophytes, 5% copepods, 4% diatoms, 65% Ice algae, and 22% other phytoplankton.

The krill Juvenile stage represents krill has passed the last furcilia stage and resembles the adult, although it is sexually immature (FAO, 2011). This starts in the model at 8 months, as it is estimated that it takes krill 85 days to reach the F3 phase (Ideka, 1984; Siegel et al., 2005), and then more time to reach the F6 stage. As furcilia develop into juvenile krill, they retain their association with the sea ice as they move into their second winter (Daly and Zimmerman, 2004). Juvenile krill are not targeted by the fishery, but they are often caught as bycatch when targeting the larger krill. The juvenile and adult stages also feed on phytoplankton during the ice free season and ice algae during the winter, being most abundant under the rough ice where they can access ice algae and hide from predators (Marschall, 1988). Feeding rates for juveniles and adults are lower in winter, as they reduce their metabolism and size in order to survive the winter Atkinson et al. (2002). Juvenile krill feed predominantly on phytoplankton, with diatoms being the most abundant item found in stomach contents of juveniles and adults (Atkinson et al., 2002; Schmidt et al., 2006). Other important prey items in the summer months include tintinnids (micro-zooplankton), large dinoflagellates, and other armored flagellates while copepods were considered rare (Schmidt et al., 2006). Juvenile and adult phases can switch to carnivorous food sources such as copepods (Cripps and Atkinson, 2000) Atkinson et al. (2002), most likely occurring when plankton biomass is reduced. Diel migra-

tions allow krill to feed on the meso-zooplankton community and helps them to avoid predation during daylight hours (Hernandez-Leon et al., 2001). The diet for this group was set to 2% macro-zooplankton, 2% micro-zooplankton, 1% cryptophytes, 18% copepods, 12% diatoms, 37% Ice algae, 3% other phytoplankton, and 25% detritus.

The adult krill phase represents all sexually mature krill. Individuals mature and begin mating at two years of age (FAO, 2011), while some males do not reproduce until their third year (Siegel and Loeb, 1994). and can live up to seven years and grow up to 65cm (Reid, 2001). The krill fishery operated primarily on this stanza group. Adult krill can reduce their metabolism and size in the winter to conserve energy (McGaffin et al., 2002; Meyer et al., 2010). Feeding studies at the onset of winter indicate the diet is dominated by small copepods with a general trend toward omnivory in the winter months (Atkinson et al., 2002; Meyer et al., 2010). The diet for this group was set to 1% juvenile krill, 0.001% larval krill, 0.001% krill embryo, 8% macro-zooplankton, 1% micro-zooplankton, 2% cryptophytes, 36% copepods, 12% diatoms, 35% ice algae, 3% other phytoplankton, and 2% detritus.

The biomass of krill varies over years and seasons. For an area west of the Antarctic Peninsula estimates for the 1993-1994 season range from spring ($32 \text{ g}\cdot\text{m}^{-2}$) summer ($95 \text{ g}\cdot\text{m}^{-2}$) fall ($12 \text{ g}\cdot\text{m}^{-2}$) and winter ($8 \text{ g}\cdot\text{m}^{-2}$) (Lascara et al., 1999). Elephant Island showed a low biomass of $0.98 \text{ g}\cdot\text{m}^{-2}$ for the 90/91 summer to a high of $31.16 \text{ g}\cdot\text{m}^{-2}$ for the 77/78 season (Siegel et al., 1998). Various samples Antarctic wide are summarized in (Siegel et al., 2005) with biomass at the peninsula ranging from 8-138g/m² depending on the year and method of sampling (acoustic vs. net). A summary of multiple krill samples spanning the Antarctic in the krill/salp database (Atkinson et al., 2004), estimated the Antarctic Peninsula biomass to be $37.66 \text{ g}\cdot\text{m}^{-2}$ in 1978. While this estimate likely only represents the adult and juvenile stages, the leading or adult krill biomass was set to $9.080 \text{ t}\cdot\text{m}^{-2}$, so that the total krill biomass was $35.22 \text{ t}\cdot\text{m}^{-2}$.

Krill can live up to and in some cases more than 6 years (Pakhomov, 1995a). Mortality ranged from 0.52 y^{-1} for mature stages of krill, to 1.1 y^{-1}

J.1. Model Parameters by Functional Group

for the first year, 2.41y^{-1} for the last years of life. Survival at the Antarctic Peninsula averaged $0.36\text{-}0.41\text{y}^{-1}$ (for age classes 2+), but can range from $0.4\text{-}0.78\text{y}^{-1}$. At south Georgia krill grow at high rates from October- March (austral summer) indicating growth rates are higher than predicted by existing models (Reid, 2001).

Based on the values in table J.7, the P/B values used for krill groups were set to; 1.5y^{-1} for adults, although higher than the natural mortality rates from other areas, it was increased to account for fishing. The juvenile group was set to 0.9y^{-1} , and accounts for a small amount of fishing mortality. The Larvae group was set to 2.5y^{-1} and the embryo class was set to 8y^{-1} , higher than the year 1 values, but since these age classes are so short, and highly reliant on environmental conditions, it was assumed they would have higher mortality rates than krill that reach the juvenile phase.

Table J.7: Natural mortality rates (y^{-1}) of Antarctic krill (*Euphausia superba*) for areas north and south of the Antarctic divide (AD) for the Cosmonaut and Cooperation Seas. Values taken from Pakhomov (1995b).

Age	S of AD Cooperation Sea	N of AD Cooperation Sea	Cosmonaut Sea and S AD
1	1.1	1.12	1.09
2	0.65	0.64	0.65
3	0.55	0.52	0.57
4	0.7	0.54	0.77
5	1.29	0.95	1.54
6	-	2.41	-

Consumption rates were calculated to be of 5% of body carbon per day based on fecal pellets or 0.4-1.7% of body carbon from gut florescence, from Feb-March at South Georgia (Pakhomov et al., 1997). Over a 100 day growing season this could range from $40\text{-}500\text{y}^{-1}$. These were from the 38-42mm length indicating they were of the adult size class. As a conservative estimate the Q/B for adult krill was set to 33y^{-1} .

In addition to the curvature parameter (Von Bertalanffy growth K parameter), a recruitment power parameter was set to 1. Lower values 0.1-0.5 indicate juveniles spend time outside the model area where density depen-

Table J.8: Multistanza parameters for krill functional groups.

	Group	Start Age (months)	B	Z	Q/B
51	Krill Larvae	0	0.006	8	698.506
52	Krill Juvenile	2	0.879	2.5	149.443
53	Krill sub-adult	8	25.26	0.9	49.481
54	Krill Adult	36	9.08	1.5	33

dence may affect mortality (Christensen et al., 2005). As krill are spawned and hatched within the model area, the value was set to the default of 1. A weight at maturity (W_M) vs weight at length infinity (W_∞), the weight of fish at the asymptotic length (L_∞), is included with weight at length infinity equal to the length at size infinity cubed or $W_\infty = L_\infty^3$. L_∞ was set to 65mm (Reid, 2001), with length at maturity set at 37.5mm based on female krill reaching L_{50} at 34.65-35.9mm²² and males reaching L_{50} 43.35-43.71mm (Siegel and Loeb, 1994) to give a ratio of 0.190.

Macro-zooplankton and Other Meso-zooplankton

The macro-zooplankton group contains all zooplankton larger than the 0.2mm size with the exception of krill (Euphausiids), salps (tunicates), and copepods. Noted in literature were Ostracods, Amphipods, Mysids, Ctenophores, Cnidarians, Polychaetes, Chaetognaths, Molluscs, and various larvae (Hopkins, 1985; Calbert et al., 2005). Macro-zooplankton samples from Gerlache Strait and Bransfield Strait within the model area indicate macro-zooplankton biomass ranging from 0.141-6.99g·m⁻² (Calbert et al., 2005). Zooplankton groups(meso and macro) from Croker Passage in 1983 were estimated to be 19.07g·m⁻² (Hopkins, 1985). While these estimates represent values in the summer when biomass is higher, the annual value was set to 8.170t·km⁻².

The EE was set to 0.95, and the P/Q was set to 0.3 to allow the model to estimate the PB and QB values. Diet from other studies: suggest a variety of food sources including ice algae, other phytoplankton, and smaller

²² L_{50} is defined where 50% of the population reaches sexual maturity

zooplankton (Moline et al., 2004; Peck et al., 2005). The diet for this group was set to: 2% adult krill, 4% juvenile krill, 5% micro-zooplankton, 10% cryptophytes, 2% copepods, 21% diatoms, 35% ice algae, 15% other phytoplankton, and 6% detritus.

Micro-zooplankton

Micro-zooplankton is thought to be an important part of Antarctic food webs, and a source of prey for krill (Froneman et al., 1996). Surveys of nano and micro-zooplankton from the Weddell sea in summer indicate levels of $0.3\text{--}0.6\text{gC}\cdot\text{m}^{-2}$ (or $2.49\text{--}4.98\text{g}\cdot\text{m}^{-2}$) (Garrison et al., 1991). The biomass for the model was set to a conservative value of $2.9\text{t}\cdot\text{km}^{-2}$. The the Q/B was set to 110y^{-1} , slightly higher than the copepod value, with an assumed P/B value of 65y^{-1} . The diet was assumed to be 15% cryptophytes, 25% diatoms, 20% ice algae, 35% other phytoplankton, and 5% detritus.

Copepods

This group includes numerous species of copepods (see Hopkins, 1985, for a detailed list of copepod species). Copepods are an abundant zooplankton species in the Antarctic, and serve as a food source for krill, other zooplankton, fish, and even birds. Biomass of copepods was sampled at $15.14\text{g}\cdot\text{m}^{-2}$, in South Georgia and from $4.53\text{--}23.12\text{g}\cdot\text{m}^{-2}$ in the Bellingshausen Sea (Calbert et al., 2005). Estimates at South Georgia range from 1 to $13\text{g}\cdot\text{m}^{-2}$ for one species *C. acutus* (stages CIV and CV only) should be considered low, as these stages are thought to only represent 25% of the total copepod biomass at South Georgia (Shreeve et al., 2005). The model biomass was set to $15.2\text{g}\cdot\text{m}^{-2}$ for all copepod species, based on samples from South Georgia.

The P/B ratio from South Georgia was estimated at about 10y^{-1} for CIV and CV stages of *C. acutus* based on Shreeve et al. (2005), although this parameter was ultimately estimated by the model. Consumption from daily uptake rates indicate a range from 2.5–5.4% of body weight per day as measured by carbon, however values for the Southern Ocean can range from 1–20% of the body weight per day for various copepod species (Metz

and Schnack-Schiel, 1995). When converted to annual rates, consumption of 1-20% of body weight a day would be 3.65 to 73, although copepods are not actually feeding every day of the year. It is likely that smaller copepods not included in the study would have higher annual Q/B rates, but the group Q/B was set to 50y^{-1} . The EE value was set to 0.95. Studies of *Calanoides acutus*, *Rhincalanus gigas* and *Calanus propinquus* indicate diet is primarily comprised of protozoans, micrometazoans, autotrophs and can include other zooplankton (Bathmann et al., 1993) Metz and Schnack-Schiel (1995). The diet was set to: 15% micro-zooplankton, 35% diatoms, 25% ice algae, 20% other phytoplankton, and 5% detritus.

Primary Producers

Primary producers were split into four groups in order to account for their different roles in the food web. Research has identified the linkages between cryptophytes blooms and lower salinity water, as well as diatoms and higher salinity waters (Moline et al., 2000, 2004). Diatoms and cryptophytes have been shown to be the dominant phytoplankton for the region in the summer months with diatoms having a strong association to sea ice (Varela et al., 2002; Garibotti et al., 2003; Moline et al., 2004), thus demonstrating their importance to the food web. With the intent of exploring how the different types of producers affect the system as a whole and how these issues relate to krill, salps, and other consumers in the food web, primary producers were split into cryptophytes, diatoms, other phytoplankton, and ice associated algae. All producer groups are considered to be associated with open water with the exception of the sea ice. Biomass for phytoplankton was given for summer months. Annual average values needed for model input were assumed to be 1/3 of the summer biomass. In addition production values were calculated annually, but based on 120 day growth period (Smith et al., 1998), to account for the high seasonality of the area.

Cryptophytes

Cryptophyte abundance has been shown to be correlated with lower salinities in the Antarctic Peninsula (Moline et al., 2000), making it a potentially critical base for the food web in the event that climate change increases or continues in the future. Biomass ranges for this group were as high as $21.6\text{t}\cdot\text{km}^{-2}$ for summer values in highly concentrated areas (Varela et al., 2002), but reduced to $5.4\text{t}\cdot\text{km}^{-2}$ when accounting for the whole study region. Others (Garibotti et al., 2003) estimated the summer biomass to be roughly $6\text{t}\cdot\text{km}^{-2}$ for the summer season. The average yearly biomass was set to $2.2\text{t}\cdot\text{km}^{-2}$. The production for this group was set to 75 y^{-1} based on a 120 day summer season for growth with published production rates ranging from $0.5\text{--}1.5\text{ g C}\cdot\text{km}^{-2}\cdot\text{day}^{-1}$ (Varela et al., 2002), however it was increased to 80y^{-1} to balance the model.

Diatoms

This group contains all diatoms not associated with the sea ice. The biomass was sampled to range from $130\text{ ug C}\cdot\text{l}^{-1}$ (Garibotti et al., 2003) and was converted to a summer biomass range of $40.9\text{g}\cdot\text{m}^{-2}$ (wet weight). The annual biomass was reduced to $1/3$ of the summer biomass to give $13.65\text{t}\cdot\text{km}^{-2}$, which was slightly lower than the regional average of roughly $21\text{t}\cdot\text{km}^{-2}$ for the WAP region calculated by (Varela et al., 2002). The final value used for the model was set to $17.41\text{t}\cdot\text{km}^{-2}$ to balance the model. The production of diatoms was converted from $0.87\text{--}4.54\text{ g C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (Varela et al., 2002) to give a P/B range of $22.5\text{--}117.4\text{y}^{-1}$. The value of 90.51y^{-1} was used to balance the model.

Ice Algae

This group contains all phytoplankton which is associated with the sea ice. Species known to exist in the ecosystem are chrysophytes, diatoms, dinoflagellates, cryptophytes, ciliates, choanoflagellates, prasinophytes, and prymnesiophytes (Garrison and Buck, 1989), as well as bacteria. Biomass

estimates were converted from chl a to wet weight using conversions provided by Cauffope and Heymans (2005). A late winter biomass of $3.2\text{t}\cdot\text{km}^{-2}$ was provided by Kottmeier and Sullivan (1987) was slightly lower than the $5.67\text{t}\cdot\text{km}^{-2}$ estimate from Smith et al. (1998). Based on the winter chlorophyll concentration in ice cores and newly formed ice Garrison and Buck's 1989 estimate of roughly $21\text{t}\cdot\text{km}^{-2}$ is still lower than the highest reports that Chl a concentrations can be as high as $0.4\text{g}\cdot\text{m}^{-2}$ or about $140\text{g}\cdot\text{m}^{-2}$ (Arrigo et al., 1997). The average yearly biomass was set to $25\text{t}\cdot\text{km}^{-2}$. Winter production values for ice algae ranged from $0.017\text{gC}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (Lizotte, 2001) to $0.035\text{gC}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ((Kottmeier and Sullivan, 1987) to $1\text{gC}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (Arrigo et al., 1997). Summer production values were much higher at $1.6\text{gC}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (Smith et al., 1998). At the maximum summer production values of $1.6\text{gC}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (for 120 days of summer) would yield an annual rate of 69.12y^{-1} , while winter rates of $0.017\text{gC}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (for 245 days) would yield an annual rate of 1.49y^{-1} . A value of 45.00y^{-1} was used for the Ecopath model.

Other Phytoplankton

The other phytoplankton group contains all primary producers not associated with the sea ice with the exception of diatoms and cryptophytes. This included chlorophytes, dinophytes, crysophytes, unidentified phytoflagellates, and bacterial contributions to primary production, generally present in the summer months. The average annual biomass was set to $5.5\text{t}\cdot\text{km}^{-2}$ based from a summer value of $27.9\text{ugC}\cdot\text{l}^{-1}$ (Garibotti et al., 2003). P/B increased from the calculated value of 77.4y^{-1} (from $0.21\text{gC}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) (Varela et al., 2002) to 105y^{-1} to balance the model.

Detritus

Detritus biomass was calculated using the following equation from Pauly et al. (1993):

$$\text{Log}_{10}D = -2.41 + 0.954\text{Log}_{10}PP + 0.863\text{Log}_{10}E \quad (\text{J.8})$$

where D is the standing stock of detritus ($\text{g C}\cdot\text{m}^{-2}$), PP is primary productivity ($\text{g C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$), and E is the euphotic depth in meters. Estimates of primary production for the area ranged from $0.36\text{gC}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ (Vernat et al., 2008) for offshore areas to $55\text{--}425\text{gC}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ (Smith et al., 2001) for areas near Palmer Station. A primary production value of $0.4\text{gC}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ was used to calculate the detritus biomass along with a photic depth of 25 meters based on the depth of the upper mixed layer ranging from 13-23m for the 1995-1996 summer (Varela et al., 2002) and 30-35m for later in the 1996 summer season (Garibotti et al., 2003). This resulted in a detritus estimate of $3.43\text{t}\cdot\text{km}^{-2}$ of detritus.

J.2 Ecosim Input Parameters

Fisheries

Krill Fishery

For this model the "krill fishery" is classified as mid-water otter trawls as cited in the CCAMLR statistical Bulletin (CCAMLR, 2008b). Catches (figure J.3) were provided and applied to adult and juvenile krill groups as the mesh size of the trawls is not capable of catching the smaller size classes. Krill fishing in the AP show that most catches are obtained from the shelf area in depths less than 1000m (Murphy et al., 1997), where they are likely competing with land based marine mammals and birds. Effort for this fishery was driven using the total number of fishing hours (figure J.2). However in the fitting process, catch time-series was used as forced values, thereby negating the effort driver.

Other Fishery

The "other fishery" includes all other species caught over the time period of the model 1978-2007. This includes exploratory fishing for toothfish species, and general fishing that occurred on any species other than krill in this area. Catches for the first year of the model were set to $1\text{E-}05\text{t}\cdot\text{km}^{-2}$ for each of the following groups in which at least one species was fished throughout

the time series; Other Icefish, Toothfish, Large Nototheniidae, Small Nototheniidae, Myctophids, Other Pelagics, *C. gunnari*, *P. antarcticum*, and *N. gibberifrons*. This value was set low, as there were no recorded catches in 1978, however 1979 had the highest landings and effort for the entire time-series. This fishery mostly includes test fisheries on finfish species with some by-catch. As all species caught in the test fishery are reported, and broken down by species. Effort (fishing hours) was used to drive the catches of these species (figure J.2), however, this did not reproduce the pattern of catches (figure J.3) for the various fish species, so catches were entered for each functional group and used in the fitting process. All fishery data was obtained from CCAMLR records on the digital database (CCAMLR, 2008b).

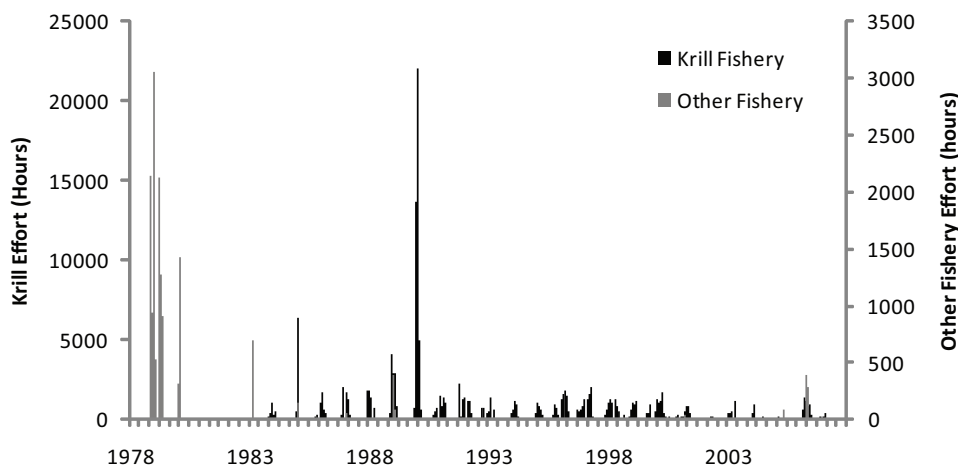


Figure J.2: Krill fishing effort used in model fitting for the krill fishery and the other fishery representing fish catches. Data provided by CCAMLR (2008b).

Abundance Trends

In addition to krill catch and effort, biomass and abundance trends were provided by multiple sources for varying time spans. These trends were used to fit the model using either abundance (Atkinson et al., 2004; Quetin

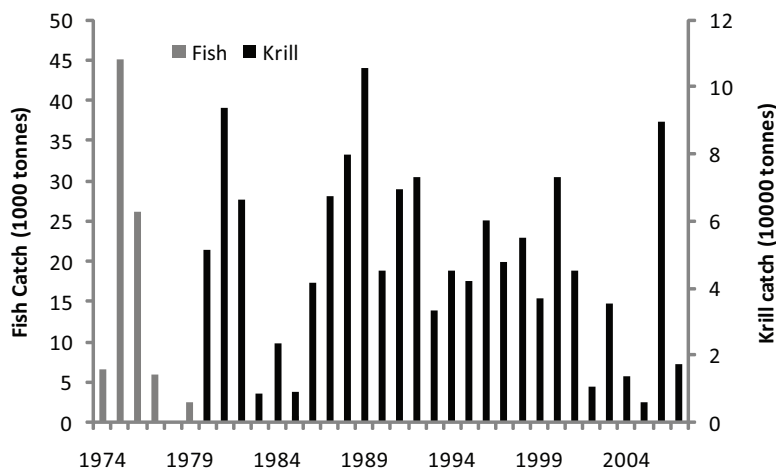


Figure J.3: Krill catches used in model fitting for the krill fishery and the other fishery representing fish catches. Data provided by CCAMLR (2008b).

and Ross-Quetin, 2006), or biomass (Siegel et al., 1998, 2002). However ultimately the KRILLBASE (Atkinson et al., 2004) data was used, as it provided the most complete geographic and temporal time-series trend for krill (figure J.4).

For salps, two potential data sets were available for abundance trends; the KRILLBASE dataset (Atkinson et al., 2004), and a dataset from PALMER station (Quetin and Ross-Quetin, 2006). Again the KRILLBASE dataset was chosen as it was more complete (figure J.5) .

Adelie, Chinstrap and Gentoo penguin abundance trends were taken from the Palmer Long Term Ecological Research Data (Fraser 2006), based on the number of breeding pairs around Palmer Station on Anvers Island, Antarctic Peninsula. While adelie penguins have occupied Palmer Station at the Antarctic Peninsula for over 700 years, the first chinstrap colony at Palmer Station was established in 1974, and the first gentoo arrival was not until 1994 (McClintock et al., 2008). Each penguin species has a different relationship to the climate, sea ice, and the changes in food availability. For example, it is believed chinstrap and gentoo penguins avoid areas with persistent sea ice as a majority of their populations are based in sub-Antarctic

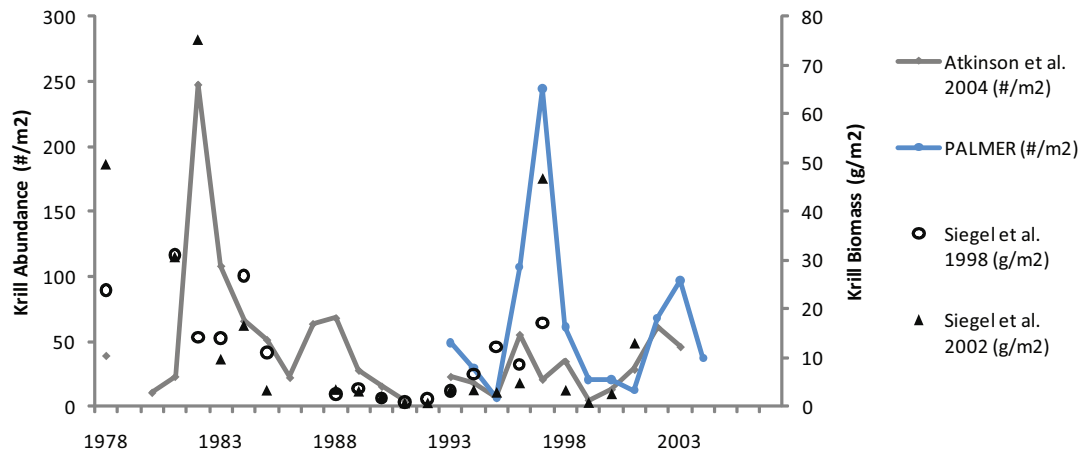


Figure J.4: Krill abundance and biomass trends from the Antarctic Peninsula

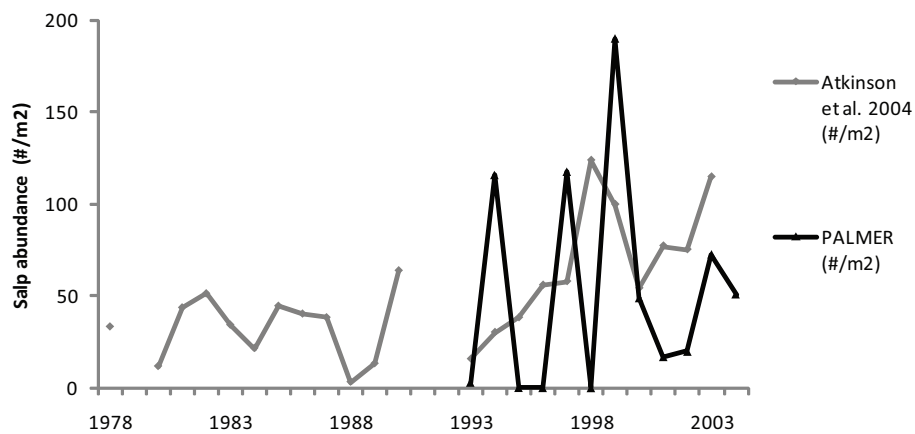


Figure J.5: Salp abundance trends from the Antarctic Peninsula.

areas, and they most likely evolved in conditions with open water a majority of the year (McClintock et al., 2008). Adelie penguins on the other hand, are quite dependant on winter sea ice through the krill that is supported by the ice. It has been suggested that at the Antarctic Peninsula sea ice has declined past an optimum point for adelie penguins, and this is the cause for the declining population (Croxall et al., 2002). Emperor penguins have also been shown to decline as much as 50% since the 1970 in eastern Antarctica (Terre Adelie; Indian Ocean sector) which has been correlated to reduced sea ice in the same area (Barbraud and Weimerskirch, 2001), however datasets for emperor penguins are lacking for the Antarctic peninsula.

Table J.9: Summary of time-series data used to fit the model.

Time series data	Type of data used	Reference
Krill Abundance	Relative Abundance	Atkinson et al. (2004)
Krill Catch	Forced Catches	CCAMLR (2008b)
Krill Effort	Effort	CCAMLR (2008b)
Salp Abundance	Relative Abundance	Atkinson et al. (2004)
Other Fishery Catch	Forced Catches	CCAMLR (2008b)
Other Fishery Effort	Effort	CCAMLR (2008b)
Adelie Abundance	Relative Abundance	Fraser (2006)
Gentoo Abundance	Relative Abundance	Fraser (2006)
Chinstrap Abundance	Relative Abundance	Fraser (2006)

Forcing Functions

Three forcing functions (FF) were used to fit the model: sea surface temperature (SST), sea ice cover (% cover), and the southern oscillation index (SOI). The SST and ice cover time-series were extracted from the HadISST (Hadley Centre Sea Ice and Sea Surface Temperature data set) model by month (BADC, 2010) for cells within area 48.1. The model data is presented as the monthly average for $1^\circ \times 1^\circ$ cells for the world, with the values for the Antarctic Peninsula used as the mean of all cells within the area (figure 3.3).

The Southern Oscillation Index (SOI) used in the model is calculated using the difference in air pressure between Tahiti and Darwin, Australia. Pos-

itive values indicate cold ocean temperature, higher air pressure in Tahiti, and lower air temperature in Darwin. Negative values indicate, lower air pressure in Tahiti, higher air pressure in Darwin, and warmer waters. Positive values are generally associated with La Nina years, while negative values are associated with El Nino years. SST is also affected by the changes in pressure, however the SOI may give better insight as to factors determining salp abundance and was therefore tested as a driver. Values for the SOI (figure 3.3) were taken from the PALMER station dataset (Stammerjohn, 2007). All forcing functions were re-scaled so that the average of the first year of the model (1978) was scaled to 1.

Ice cover was used as a FF for ice algae within the model, as well as diatoms. Ice algae remain in the sea ice overwinter and are utilized by predators such as krill throughout the winter (Marschall, 1988; Arrigo et al., 1997). Diatoms are favored in cooler years associated with higher sea ice, and are often an important component of sea ice algae, forming blooms at the ice edge when melting commences (Legendre et al., 1992). Ice cover as a forcing function for both of these functional groups provided a better fit (reduction to sum of squares value) to the krill functional groups. In addition sea ice was used as a FF for ice algae predators, applied to the arena area for each predator. The ecological interpretation is that as ice cover increases, so does the arena area for predators to feed on ice algae.

SOI and SST were used under different fitting attempts (A and B respectively). Forcing functions (FF) for cryptophytes and the other phytoplankton functional groups, as cryptophytes have higher biomass in warmer years (Moline et al., 2004), and the other phytoplankton group was created to represent species associated with the spring bloom. The SST pattern follows a similar pattern to summer bloom and ice free conditions important to warmer water producers. Salps tolerate warmer water than krill (Atkinson et al., 2004), with higher prevalence of salps potentially linked to warming waters being advected in the area (Pakhomov and Froneman, 2004). By applying these forcing functions to the cryptophytes and other phytoplankton functional group, we were able to fit the time-series of salps to model.

Other environmental time-series were tested in the fitting of the model,

but did not produce optimal results. Data from the PALMER LTER study of sea ice extent, and open water extent, and air temperature were considered (Stammerjohn, 2007). While sea ice extent did provide comparable results (once both FF were re-scaled to average 1 for the first year) to the ice cover FF, future data is available for percentage ice cover, therefore it was selected over ice extent.

Mediation Functions

While forcing functions were helpful in fitting the model to past data, mediation functions were added to decrease SS values for both fittings, and include indirect ecological relationships. A mediation function was also applied to krill to represent the protection sea ice can provide from predators (figure J.6). Krill have been observed by SCUBA divers to retreat into crevasses in sea ice for protection (Marschall, 1988). A mediation function was created so that as the biomass of ice algae increases, krill become less vulnerable to their predators, with a large decline as ice decreases from the starting values within the model, and tapering impacts from low to extremely low ice cover. This mediation function was applied to both the larval and juvenile stages of krill under both fitting scenarios (SOI and SST).

Sea ice was also used in a mediation function for salps. As salps are pelagic organisms with the abundance higher in warmer years with lower sea ice (Moline et al., 2004; Nicol, 2006), the mediation function used indicated as sea ice decreased (as determined by ice algae), the foraging area of salps increased using a linear relationship (figure J.7). This mediation function was applied to all prey groups of salps under both fitting scenarios (SOI and SST).

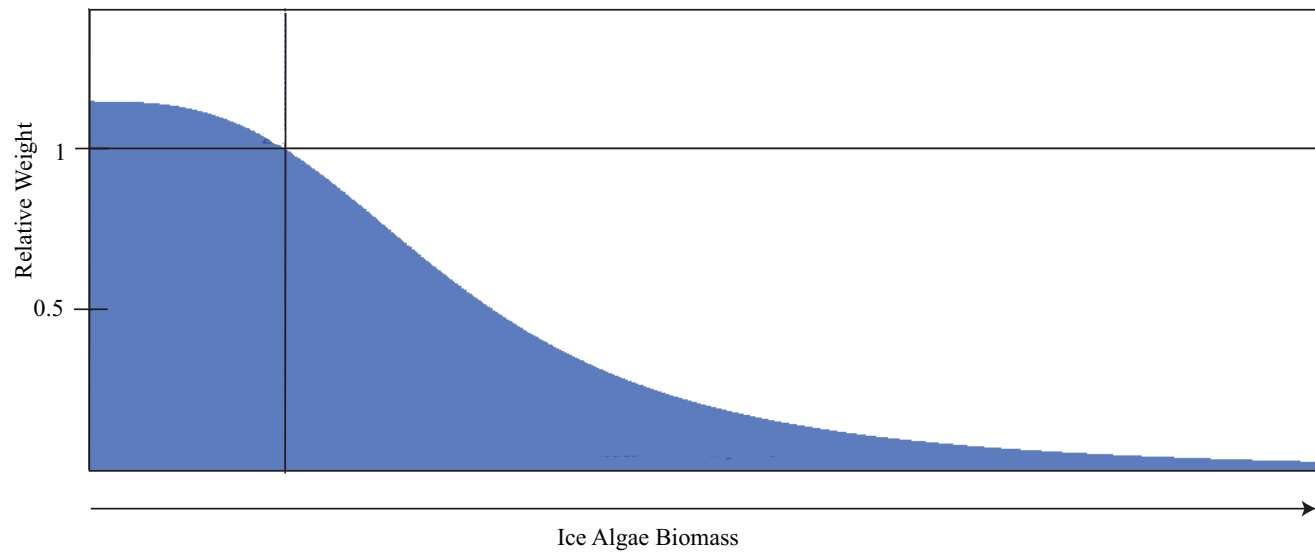


Figure J.6: Mediation function for larval and juvenile krill. As ice algae biomass increases krill groups become less vulnerable to predators.

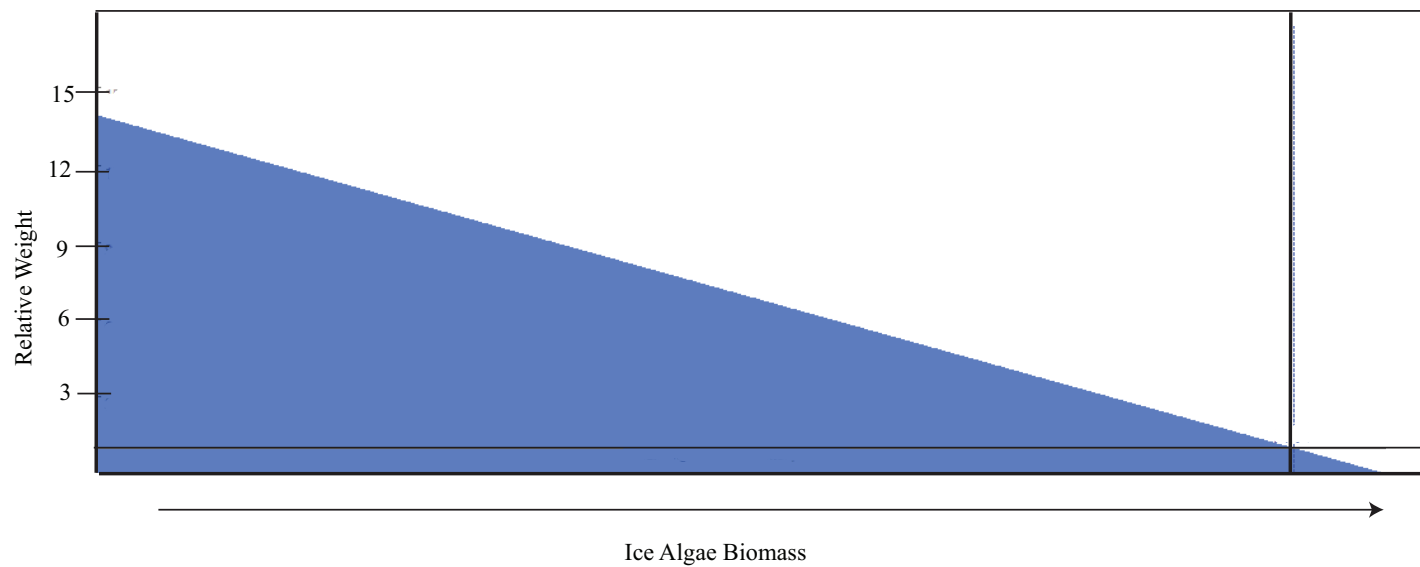


Figure J.7: Mediation function used for the salp functional group. As ice increases (as determined by the biomass of ice algae) the foraging area for salps decreases. This was applied to all prey groups of salps.

A mediation function to replicate salps dying at high food concentrations was tested to see if it would improve the fit. Therefore a mediation function was used for salps based on the idea that at high food concentrations the mucous nets which are used for feeding become clogged with food particles. This renders the salps unable to continue feeding and causes death in lab experiments for the salp, *Pegea confoederata* (Harbison et al., 1986). A mass stranding of *Salpa thompsoni* near the Antarctic Peninsula in 2002 was linked to high wind conditions transporting nutrients and re-suspending detritus, thereby causing high particle concentrations and leading to the clogging and death of the salps (Pakhomov et al., 2003). The mediating group for salps was chosen to be the other production group, as this and cryptophytes were driven by temperature or SOI, depending on the fitting scenario. As cryptophytes are smaller in size, and generally less abundant in the model on an annual basis, it was assumed the larger more abundant other phytoplankton group would do more damage to clogging salps. The mediation function was applied to the search rate of salps on other phytoplankton and cryptophytes, so as the biomass of other producers increase, the search rate will also increase to a certain point and then drop off. This pattern was selected, as not all salps become clogged at the same food concentrations (Harbison et al., 1986). While this mediation function did improve the SS value initially, the sea ice mediation function provided a lower SS value. The combination of both mediation functions of salps did not decrease the SS value lower than the sea ice mediation function alone, so the clogging function was removed from the model.

Biomass Accumulation

Biomass accumulation was added to the chinstrap and gentoo penguin groups, based on increases to populations in the model area. Please refer to the individual functional group descriptions for values and ecological relevance.

Group info Parameters

The maximum relative feeding time is the amount of time a predator can increase their foraging time if prey becomes scarce. The default value for functional groups is set to 2, but can be increased for species which are able to increase their (Christensen et al., 2005)(Christensen et al., 2007). The value was increased for land based predators, as they can increase their foraging time by spending less time on land. A value of 10 was used for whales (killer, sperm, blue, fin, minke and humpback), and a value of 5 was used for seals (leopard, Ross, Weddell, crabeater, southern elephant and Antarctic fur seal).

The feeding time adjustment rate parameter was set to a default value of 0, indicating a constant feeding time (along with a constant risk to predation). This parameter can range from 0 to 1, with 1 indicating fast responses in adjusting feeding times as to stabilize the consumption (Q/B) (Christensen et al., 2005, 2007), meaning a predator respond faster to feed more in lower food concentrations as to regulate the Q/B ratio set in the model. A recommended value of 0 was used for all model groups with the exception of marine mammals and birds. The recommended value for marine mammals is 0.5, which was used for all whale and seal functional groups. A value of 0.2 was used for penguins and flying birds, as they can regulate the amount of time spent in the water foraging.

Vulnerabilities

Vulnerabilities were estimated by Ecosim using the fit to time series routine (Buszowski et al., 2009). This routine searches for vulnerabilities which lower the overall sum of squares. Further manipulation of key predator prey interactions was done to see if model fit was improved. In cases where adjustment of individual interactions provided a better model fit, the adjusted values remained. It should be noted that several iterations of the vulnerability search and manual manipulation of vulnerabilities was done under a variety of forcing functions and time series data (various krill and salp trend, SOI, sea ice cover, sea ice extent, SST, and air temperature) before

final selections were made. Final vulnerabilities are presented in appendix K.

J.3 Model Parameterization and Output

Ecopath Model Balancing

In the Ecopath phase, changes were made to parameters in order to ensure the model could be balanced before moving onto the Ecosim portion. General changes made to the model were:

1. The consumption rates of some marine mammals were too high, and had to be lowered in the balancing process. The high consumption values calculated caused the EE for predators such as other marine mammals, fish, and penguins to be over 1. In most cases the Q/B value reduction was small (less than 10%).
2. The P/B ratio for fish was too low as estimated by Pauly (1980). As the empirical data used to formulate this equation was based on temperate and tropical fish species and excluded polar data, it most likely underestimates the value for polar species (Palomares and Pauly, 1998). Values were increased to balance these model groups.
3. Literature indicates a very strong dietary link between predators and krill. However, even as though krill biomass (for all stages combined) was large in comparison to other organisms, the contribution to the diet of predators had to be decreased in order to balance the model.
4. The consumption of cephalopods was initially guestimated to be 10y^{-1} (Efran and Pitcher, 2005), but was lowered as the predation mortality on prey items was too great. It was lowered to 2y^{-1} in line with the cephalopod value for the Kerguelen Islands, a sub-Antarctic area (Pruvost et al., 2005).
5. Changes to the P/B and Q/B values for invertebrates. Most alterations to calculated values were increases in order to balance the

model.

J.3. Model Parameterization and Output

Table J.10: Balanced model with bolded values estimated by the model.

Group name	Trophic level	Biomass	P/B	Q/B	EE	P/Q
		($t \cdot km^{-2}$)				
Killer Whales	4.543	0.001	0.05	11	0	0.005
Leopard Seal	4.139	0.006	0.12	8.1	0.637	0.015
Ross Seal	4.123	0.004	0.13	15.3	0.83	0.008
Weddell Seal	3.972	0.021	0.17	13.88	0.689	0.012
Crabeater Seal	3.423	0.164	0.09	15.86	0.363	0.006
Antarctic Fur Seals	3.694	0.028	0.175	25	0.862	0.007
S Elephant Seals	4.25	0.006	0.165	10.37	0.437	0.016
Sperm whales	4.203	0.005	0.034	7.33	0	0.005
Blue Whales	3.41	0.001	0.032	3.53	0.683	0.009
Fin Whales	3.441	0.003	0.035	4.12	0.524	0.008
Minke whales	3.27	0.065	0.064	6.34	0.91	0.01
Humpback whales	3.343	0.02	0.04	4.12	0.963	0.01
Emperor penguins	3.871	0.005	0.15	28.69	0.933	0.005
Gentoo Penguins	3.93	0.007	0.22	29	0.642	0.008
Chinstrap Penguins	3.917	0.005	0.33	34	0.696	0.01
Macaroni Penguin	3.67	0.014	0.3	25	0.373	0.012
Adelie Penguins	3.518	0.034	0.29	30	0.793	0.01
Flying birds	3.697	0.19	0.34	14.88	0.95	0.023
Cephalopods	3.404	2.49	0.95	2	0.653	0.475
Other Icefish	3.689	0.337	0.38	1.57	0.726	0.242
Toothfish	4.228	0.046	0.165	0.77	0.627	0.214
Lg Notothenioids	3.335	0.59	0.37	1.95	0.452	0.19
Sm Notothenioids	3.332	0.341	0.65	2.2	0.873	0.295
Shallow Demersals	3.375	0.031	0.75	4.125	0.362	0.182
Deep demersals Lg	3.684	0.042	0.29	2.18	0.803	0.133
Deep demersals Sm	3.687	0.08	0.65	2.7	0.82	0.241
Myctophids	3.263	0.185	1.35	3.73	0.882	0.362
Other Pelagics	3.776	0.49	0.55	2.02	0.838	0.272
<i>C. gunnari</i>	3.391	0.29	0.48	1.8	0.475	0.267
<i>P. antarcticum</i>	3.269	1.25	1.1	3.55	0.603	0.31
<i>N. gibberifrons</i>	3.199	0.81	0.41	1.55	0.645	0.265
Mollusca	2.129	9.5	0.639	2.556	0.608	0.25

Table J.10 Continued on Next Page

J.3. Model Parameterization and Output

Table J.10 Continued						
Group name	Trophic level	Biomass ($t \cdot km^{-2}$)	P/B	Q/B	EE	P/Q
Salps	2.227	8	10	33.333	0.01	0.3
Urochordata	2.135	5.05	0.234	1	0.554	0.234
Porifera	2	12.719	0.159	0.795	0.815	0.2
Hemichordata	2	0.045	0.375	2	0.534	0.188
Brachiopoda	2.158	0.028	0.898	4.5	0.59	0.2
Bryozoa	2.108	0.491	0.475	1.75	0.98	0.271
Cnidarians	2.438	1.531	0.25	1	0.982	0.25
Crustaceans	2.374	3.613	1.05	4.2	0.888	0.25
Other Arthropods	2.929	1.01	0.616	3.326	0.981	0.185
Worms	2.438	12	0.7	3.2	0.84	0.219
Echinoidea	2.732	4.33	0.116	0.464	0.774	0.25
Crinoidea	2.428	0.164	0.125	0.8	0.523	0.156
Ophiuroidea	2.479	6.76	0.45	1.8	0.551	0.25
Asteroidea	2.345	1.778	0.231	0.924	0.774	0.25
Holothuroidea	2	5.45	0.316	1.1	0.938	0.287
Krill Adult	2.529	9.08	1.5	33	0.672	0.045
Krill Juvenile	2.25	25.26	0.9	49.481	0.788	0.018
Krill Larvae	2	0.879	2.5	149.443	0.011	0.017
Krill Embryo	2	0.006	8	698.506	0.237	0.011
Macro-Zoopl	2.154	8.17	7.577	25.257	0.95	0.3
Micro-Zoopl	2	2.9	65	110	0.982	0.591
Cryptophytes	1	2.2	80	-	0.983	-
Copepods	2.15	15.2	26.066	50	0.95	0.521
Diatoms	1	17.41	90.51	-	0.396	-
Ice algae	1	25	45	-	0.874	-
Other Phytopl	1	5.5	105	-	0.806	-
Detritus	1	3.43	-	-	0.176	-

Ecosim Fitting

The model was fit under 2 conditions: The first fitting (A) used SOI to drive cryptophytes and the other production group, and the second fitting

(B) used temperature to drive cryptophytes and other production. For both attempts at fitting the model, there was no difference to the fit of penguin groups. Declines in adelic penguins were captured through the decline of the main prey item krill. For the chinstrap and gentoo, obtaining increases in the population while food sources (krill, cephalopods, and fish). Based on increases in both populations documented, a biomass accumulation rate was added for both of these species. A rate of 5.7% a year (0.057) was used for gentoo penguins, based on increases of 5.7% at Cierva Point on the Antarctic Peninsula, and a nearly 50 fold increase at PALMER Station on Anvers Island (Quintana and Cirelli, 2000; Fraser, 2006). Even with the addition of a biomass accumulation rate in the model, the population still shows small declines.

The same is true for chinstrap penguins, even with a modest biomass accumulation rate of 10% a year, the model is not capable of capturing the data recorded from PALMER station as the surveys indicate the number of breeding pairs increased from 28 to 1288 between 1996-2004 (Fraser, 2006). In the early 1990s it was thought there was an increase in chinstrap penguins in the region due to a surplus of krill caused declines in other krill predators such as baleen whales, with some colonies increasing 6-10% per year or even higher (Fraser et al., 1992). Surveys from other breeding locations indicate mixed changes in populations; of the three study sites, one population increased, one decreased, and one fluctuated from 1980-2000 (Croxall et al., 2002) indicating the data used from PALMER station may in fact not be representative of the entire model area.

Krill were fit to the model using the mediation function for sea ice (figure J.6), and through the use of sea ice as a driver of their main food sources, sea ice algae and diatoms in addition to protection from predators. Krill abundance has been shown to be higher in years with lower sea temperature, higher sea ice extent, and higher nutrient concentrations, while the opposite patterns are observed for salps (Lee et al., 2010). Although the peak in biomass for 1983 was not captured in the model for adult krill, juvenile krill show a higher biomass than adult krill in this year. While some juvenile krill are likely caught in the samples provided by this dataset, as the adult

group is classified by sized 35mm and larger, neither group shows the highest biomass in this year. The highest adult krill biomass is shown in the model for 1992 at just over $23t \cdot km^{-2}$ while the highest biomass for juveniles was in 1988 at just over $58t \cdot km^{-2}$ for 1988, the highest biomass projected by the model for any krill group. Krill trend data indicates high biomass in 1992 and 1996, although adult krill in the model does not show high biomass in these years. Juvenile krill does have a relatively high biomass in 1996, but not 1992.

The greatest differences between the two fitted models arises from the groups where SST and SOI were used as forcing functions: cryptophytes and the other phytoplankton group. In addition salps show differences between the two fittings. For cryptophytes, both models show peaks in abundance in 1987 and 1992, however values are higher under the SST fitted model. The other phytoplankton group shows the same general trends for both fitted models, however peak abundances are higher under the SST fitted model, and low values are more extreme under the SOI fitted model. Salps show differing trends under the two fitting attempts. Under the SST fitted model a peak in biomass for 1989 is lower than for the SOI fitted model. Also the SOI fitted model generally has higher values after 1999 compared to the SST fitted model. The ending biomass for the SOI fitted model is higher for the salp group. While the SOI fitted model visually appears to fit the salp trend data better, it has been suggested recently in the literature that salp trends from 1998 onward are thought to have stabilized showing mid range abundances in recent years when compared to data from 1975-2002 (Lee et al., 2010). This is different to the data used for the model (Atkinson et al., 2004) which still shows fluctuations in salp biomass past 1998 (figure J.5). Krill and salp abundance is thought to be strongly influenced by the SOI, the ACW (Antarctic Circumpolar Wave) which brings cold deep water the surface at the peninsula, and the placement of the sACCf (Southern Antarctic Circumpolar Current Front) (Lee et al., 2010). Salp abundance has been shown to have a strong negative correlation to sea ice extent in the previous winter, which is negatively correlated to SOI (Loeb et al., 2009). SST was tested to fit the model as it is a contributing factor to both the ACW

and sACCF, although there are many other important factors contributing to the dynamics of these environmental drivers. SS values for the SST fitted model was 68.57, and SS for the SOI fitted model was 78.95. Ultimately it was decided that the SST driver provided a better fit based on SS values, with biomass trends for most species being similar (See appendix P for graphs of all functional groups).

Monte Carlo Parameter Estimation

Estimates of all parameters in the Monte Carlo routine are provided in appendix N. A summary of the biomass values obtained are provided in table J.11 along with mean and 95% CI. Graphs for biomass are provided in appendix O. CV values were assigned based on pedigree ranking of input data (Christensen et al., 2005), and are provided in appendix M. 1000 iterations were unable to improve SS value, however they did provide ranges of acceptable input parameter values.

While the CV values for marine mammals was set to 0.7 (with the exception of Ross seals), some species showed higher ranges of acceptable input parameter values. In general the model was able to support a larger range of biomass for species with higher initial biomasses (Weddell seals, crabeater seals, fur seals, minke whales and humpback whales). Ranges for penguin groups was relatively low, although the model is able to support a much higher biomass of flying birds, despite their starting biomass being higher than penguin groups. Fish groups share the same CV value, with the general trend that biomass range is proportional to starting value. *P. antarcticum* and *N. gibberifrons* have the largest starting biomasses and the largest range of acceptable biomasses, likely due to their importance to predators diets. Demersal fish (shallow and deep groups) and toothfish, show very narrow ranges of biomass. Benthic groups were assigned a CV value of 1, as input biomass was based on region specific surveys. Results indicate benthic groups with higher biomasses also have larger ranges of acceptable input values. The largest ranges are for sponges and worms, which have the largest biomasses in surveys (Jazdzewski et al., 1986; Saiz-Salinas

J.3. Model Parameterization and Output

et al., 1998; Piepenburg et al., 2002).

Copepods have the largest range of biomass for zooplankton groups. While this is not surprising given it has the lowest CV at 0.4, compared to most groups with a value of 1. Juvenile krill and macro-zooplankton have the next largest ranges. Salps in comparison to other zooplankton have a narrow range of acceptable starting biomass indicating the model cannot support a large starting biomass of salps, although the fitted model indicates higher biomasses are supported throughout the last 30 years. Results indicate the model can support higher biomasses of diatoms and ice algae, with lower biomasses of warmer water associated producers (cryptophytes and other producers).

Table J.11: Monte Carlo estimates using coefficient of variation (CV) values based on pedigree ranking. Lower and Upper limits refer to 95% CI. All biomass values are represented in $t \cdot km^{-2}$

	Functional Group	Biomass CV	Lower Limit	Mean Biomass	Upper Limit
1	Killer Whales	0.7	0.001	0.001	0.001
2	Leopard Seal	0.7	0.004	0.006	0.007
3	Ross Seal	0.4	0.002	0.004	0.006
4	Weddell Seal	0.7	0.015	0.021	0.027
5	Crabeater Seal	0.7	0.115	0.164	0.213
6	Antarctic Fur Seals	0.7	0.02	0.028	0.037
7	S Elephant Seals	0.7	0.005	0.006	0.008
8	Sperm whales	0.7	0.004	0.005	0.007
9	Blue Whales	0.7	0	0.001	0.001
10	Fin Whales	0.7	0.002	0.003	0.004
11	Minke whales	0.7	0.046	0.065	0.085
12	Humpback whales	0.7	0.014	0.02	0.026
13	Emperor penguins	0	0.001	0.005	0.009

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J.3. Model Parameterization and Output

Table J.11 Continued

	Functional Group	Biomass CV	Lower Limit	Mean Biomass	Upper Limit
14	Gentoo Penguins	0.7	0.005	0.007	0.008
15	Chinstrap Penguins	0.7	0.004	0.005	0.007
16	Macaroni Penguin	0	0.003	0.014	0.024
17	Adelie Penguins	0.7	0.024	0.034	0.044
18	Flying birds	0.4	0.095	0.19	0.285
19	Cephalopods	0.4	1.245	2.49	3.735
20	Other Icefish	0.7	0.236	0.337	0.438
21	Toothfish	0.7	0.032	0.046	0.06
22	Large Notothenioids	0.7	0.413	0.59	0.767
23	Small Notothenioids	0.7	0.239	0.341	0.443
24	Shallow Demersals	0.7	0.022	0.031	0.04
25	Deep demersals Lg	0.7	0.029	0.042	0.055
26	Deep demersals Sm	0.7	0.056	0.08	0.104
27	Myctophids	0.7	0.13	0.185	0.241
28	Other Pelagics	0.7	0.343	0.49	0.637
29	<i>C. gunnari</i>	0.7	0.203	0.29	0.377
30	<i>P. antarcticum</i>	0.7	0.875	1.25	1.625
31	<i>N. gibberifrons</i>	0.7	0.567	0.81	1.053
32	Mollusca	1	8.55	9.5	10.45
33	Salps	1	7.2	8	8.8
34	Urochordata	1	4.545	5.05	5.555
35	Porifera	1	11.447	12.719	13.991
36	Hemichordata	1	0.041	0.045	0.05
37	Brachiopoda	1	0.025	0.028	0.03
38	Bryozoa	1	0.442	0.491	0.54
39	Cnidarians	1	1.378	1.531	1.684
40	Crustaceans	1	3.252	3.613	3.974
41	Arthropod Other	1	0.909	1.01	1.111
42	Worms	1	10.8	12	13.2
43	Echinoidea	1	3.897	4.33	4.763

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Table J.11 Continued

	Functional Group	Biomass CV	Lower Limit	Mean Biomass	Upper Limit
44	Crinoidea	1	0.147	0.164	0.18
45	Ophiuroidea	1	6.084	6.76	7.436
46	Asteroidea	1	1.6	1.778	1.956
47	Holothuroidea	1	4.905	5.45	5.995
48	Krill Adult	1	8.172	9.08	9.988
49	Krill Juvenile	1	23.303	25.893	28.482
50	Krill Larvae	1	0.011	0.013	0.014
51	Krill Embryo	1	0.003	0.003	0.004
52	Macro-Zooplankton	0.7	5.719	8.17	10.621
53	Micro-Zooplankton	0.7	2.03	2.9	3.77
54	Cryptophytes	0.7	1.54	2.2	2.86
55	Copepods	0.4	7.6	15.2	22.8
56	Diatoms	0.7	12.187	17.41	22.633
57	Ice algae	0.7	17.5	25	32.5
58	Other Phytoplankton	0.4	2.75	5.5	8.25

Ecosim Output

Results for individual functional groups are presented as the average biomass over the last five years of the model fitting. Both fitting scenarios (A and B) are presented using either the SOI or SST (temp) for environmental forcing.

Changes in environmental drivers are shown to have expected effects to the lowest trophic levels. Ice algae and diatoms are favored in colder years (Moline et al., 2000), and are expected to decline as sea ice decreases and temperatures warm. The ice algae and diatom groups show little differences between the fitted models, as they are driven with sea ice for both fitting attempts (figure J.8). As these groups are large contributors to detritus, the decline in these groups drives a decline in detritus. The other phytoplankton group increases under both scenarios, however cryptophytes only

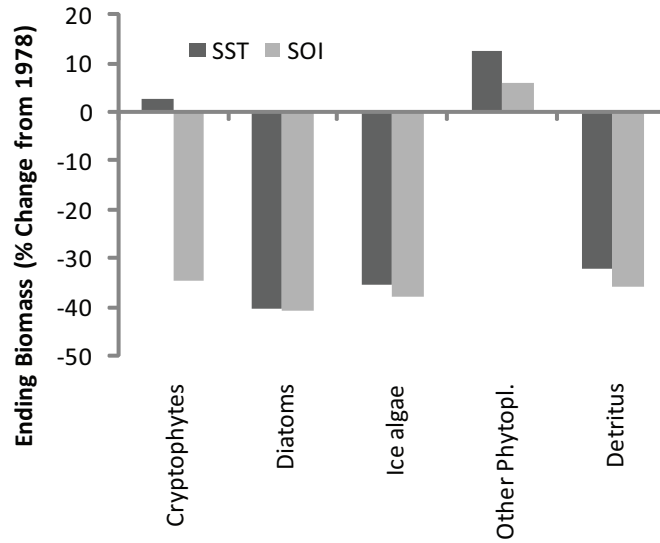


Figure J.8: Model end biomass presented as percent change from the starting Ecopath biomass for producers and detrital groups.

increase slightly under the SST fitted model. Under the SOI fitted scenario, salps have a higher biomass in the last few years of the model simulation causing increased predation on cryptophytes, thus reducing the biomass of this group. It should be noted that the SOI driver showed more extreme fluctuations from year to year, thereby causing larger changes for groups being forced with this driver. However, biomass trends for most species follow the same general pattern using different drivers, however the SOI fitted model shows more extreme annual variations. This variation in ending values for most groups is carried up the food web to higher trophic levels, most notably zooplankton. It is important to note the overall decline of detritus (of 32% and 35% for SST and SOI), which is an important factor to declines of benthic detritivores. Part of the detrital decline can be attributed to an overall decline in production (total production decreased by 31% and 34% for SST and SOI fitted models respectively).

For the zooplankton groups in the model, salps are the only group to show increases of 32% and 45% for the SST and SOI fitted models (figure

J.9). This most likely due to decreased competition, as other zooplankton groups show larger increases in the SOI scenario, salps have reduced competition for food, and the mediation function allowing salps to have larger foraging area when sea ice decreases. This is the cause for the higher biomass for the last five years of the model run. While the temperature fitted model generally provides less extreme changes to functional groups, this is not the case for the salp group. Copepods decline is caused by declines in three of their 4 food sources (diatoms, ice algae and detritus). Krill are negatively impacted by declines in their food source (ice algae and diatoms), and a reduction in sea ice which decreases protection from predators. There were large reductions in krill biomass under both fitted models with the smallest declines to the adult group. While declines appear large when compared to starting values, the cumulative krill biomass for 1978 was $37.57\text{t}\cdot\text{km}^{-2}$ with ending values of total krill biomass at 24.1 and $24.4\text{t}\cdot\text{km}^{-2}$ for the SST and SOI fitted models, resulting in declines across all stages of 36% and 37% respectively. Biomass trends do show similar trends for both models (appendix P), but the SOI fitted model shows higher biomass peaks from 1990 onward.

Decline of most benthic groups (figure J.10) is caused by decreases in detritus either as a food source causing declines, or by causing declines in other benthos which serve as prey items. For example the diet of worms was set to 60% detritus in the Ecopath model, therefore a reduction in this food source contributed to the decline of worms, which in turn contributes to the decline of other benthos. The Echinoidea group fares the best under both scenarios as predators such as worms and other arthropods decrease. The hemichordata groups shows the largest declines of 34% and 35% (for SST and SOI) due to the fact that the diet of this group is comprised completely of detritus.

All fish groups show declines under both fitted models, with the exception of myctophids (figure J.11). Fishing mortality on all harvested groups is small in relation to predation mortality, indicating fishing is not causing the declines. However declines in biomass are driven by bottom up processes in the food web. While declines appear high, biomass trends show fluctuations

J.3. Model Parameterization and Output

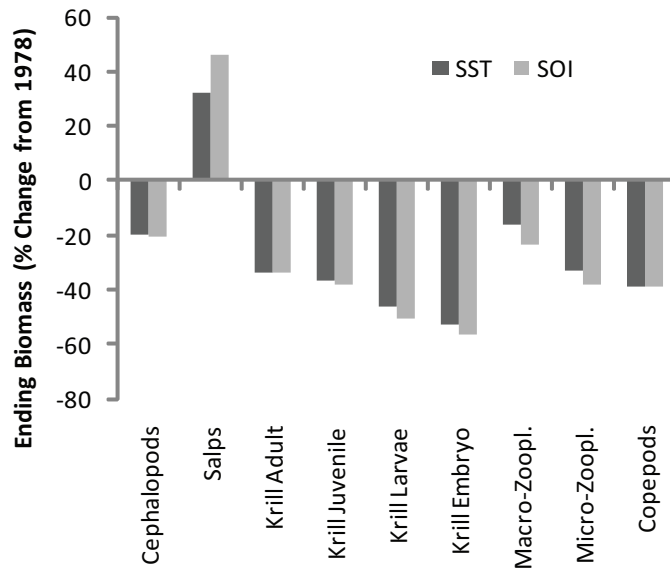


Figure J.9: Model end biomass presented as percent change from the starting biomass for zooplankton functional groups.

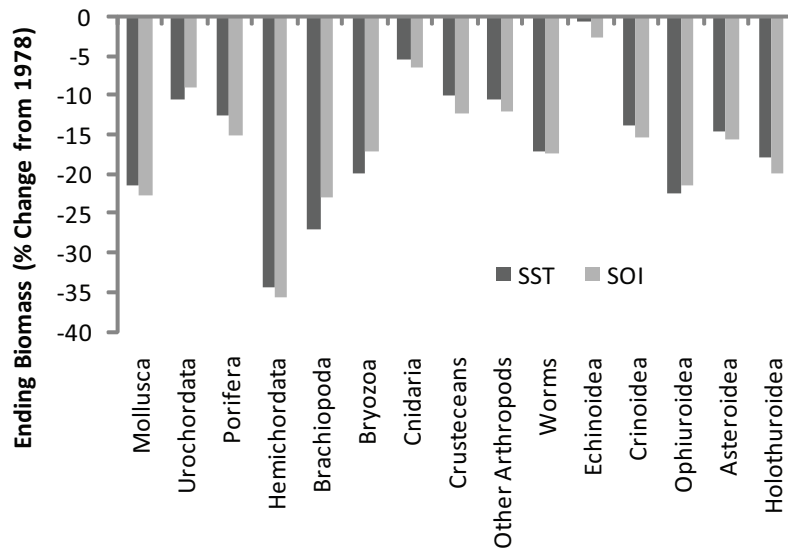


Figure J.10: Model end biomass presented as percent change from the starting biomass for benthic functional groups.

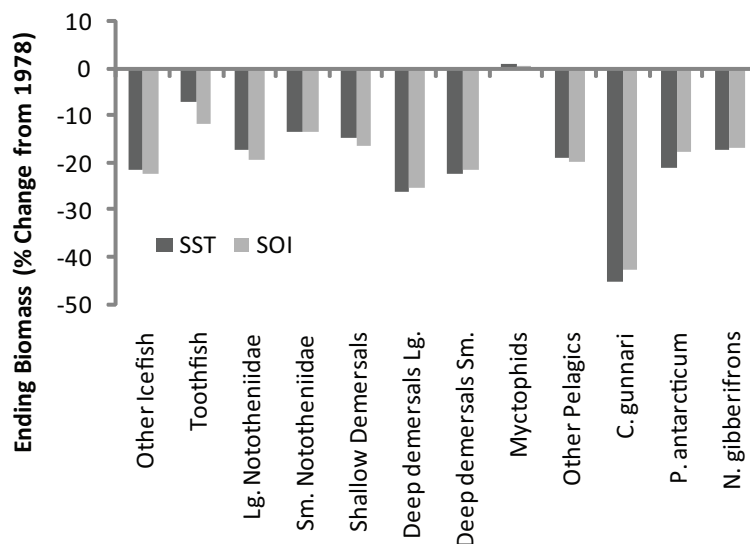


Figure J.11: Model end biomass presented as percent change from the starting biomass for fish functional groups.

throughout the simulations with the ending biomass at low values (appendix P). However, these lower biomass levels are shown to occur previously in the model simulation with most fish groups recovering to higher biomass in the mid 1990s to coincide with increases in krill. This suggests that fish populations should be able to respond to increased food conditions in the future. The myctophid biomass also shows peaks in 1988 and 1993 coinciding with peaks in juvenile krill and copepod biomasses. Although the biomass does drop off after 1999 it remains close to the starting value.

Penguins and marine mammals show varying levels of declines for both fitted models (figures J.12 and J.13). Even though biomass accumulation rates were added for chinstrap and gentoo penguins, based on increases at PALMER station (Fraser, 2006), bottom up declines in the food web cause these and other groups to decline. Krill is an important component of the diet for all of these groups. Penguins, flying birds, and cephalopods show generally declining trends with two peaks in biomass in the early 1980s and late 1990s coinciding with changes in zooplankton groups. Emperor,

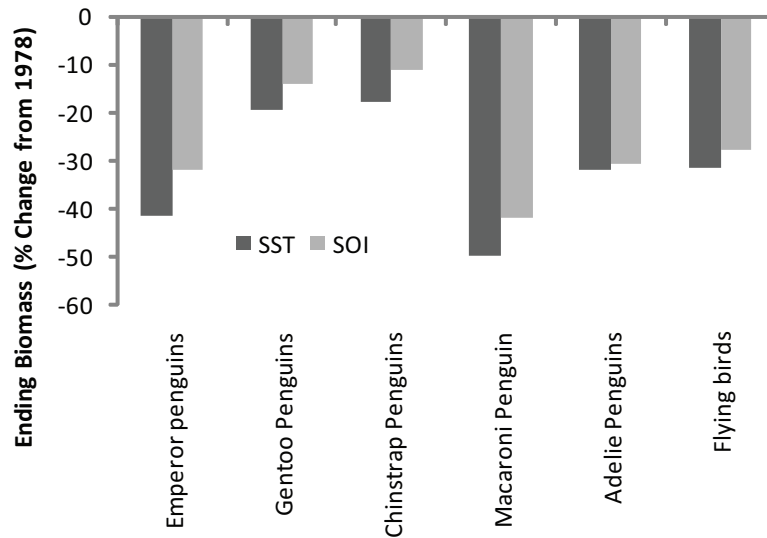


Figure J.12: Model end biomass presented as percent change from the starting biomass for bird functional groups.

chinstrap, gentoo and macaroni penguins show declines in biomass from 1984-1992 before increasing again in the late 1990s, and declining again in the early to mid 2000s. Adelie penguins also exhibit the same general trend, but biomass remains low longer, from 1984-1996, before a slight increase and then declines again in the early 2000s. Gentoo penguins at Cierva point (Gerlache Strait) showed increasing chick mortality from 1992/93 summer to 1995/95 summer with a high chick mortality in the 1995/96 summer (Quintana and Cirelli, 2000). While the authors did not link the higher chick mortality to declines in krill populations, this link has been shown for other land based krill predators such as fur seals, with krill being a likely cause for penguin declines.

Crabeater and Antarctic fur seals show the largest declines in biomass of roughly 50% and 40% for each group (figure J.13). The diet of crabeater seals is dominated by krill, as their jaws are adapted for straining krill (Lowry et al., 1998). Antarctic fur seal pups show lower survival in years of low krill abundance, specifically years where larger sizes of krill are absent in the re-

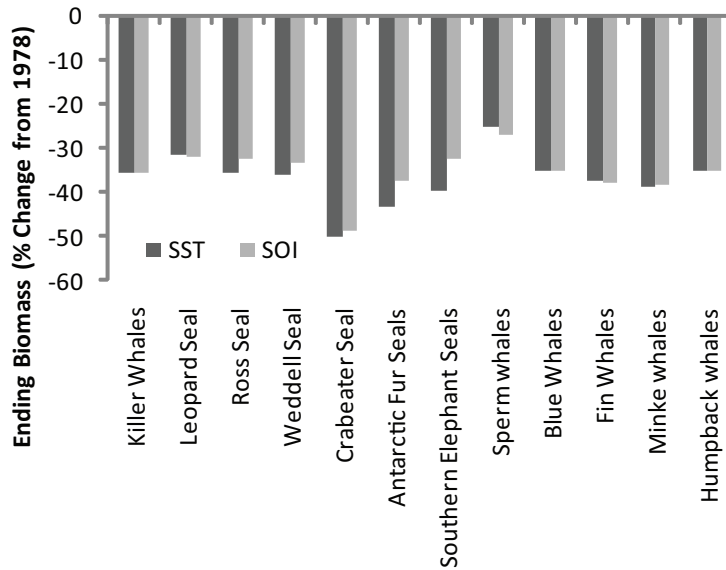


Figure J.13: Model end biomass presented as percent change from the starting biomass for marine mammal functional groups

gion, which is the preferred size of adult fur seals (Reid and Arnould, 1996). Female fur seals are dependent on local krill populations to feed while lactating (Boyd et al., 1998), reduced fur seal biomass at South Georgia in 1984 was linked to lower krill biomass in 1984, as females made longer foraging trips and higher pup mortality resulted (Costa et al., 1989). The biomass changes for Antarctic fur seals and elephant seals follow similar trends to penguins with peaks in the early 1980s and late 1990s (appendix P). However for other pinniped species (leopard seals, Ross seals, Weddell seals and crabeater seals) the rebounding biomass trend for the late 1990s is much weaker. Cetacean species show general declines over the model simulations, with little to no indication of rebounding biomasses. Long term declines in krill have the potential to cause reproductive stress or affect survival for baleen whales (Nicol et al., 2008). While issues such as reproductive stress are not incorporated into the current model, it is still important to note the declines that caused by bottom up forces within the model.

Appendix K

Antarctic Peninsula Model Vulnerabilities

Appendix K. Antarctic Peninsula Model Vulnerabilities

Table K.1: Vulnerabilities used for the fitted Antarctic Peninsula model

Prey predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Killer Whales															
Leopard Seal	2														
Ross Seal	2	2													
Weddell Seal	2	2													
Crabeater Seal	2	2													
Antarctic Fur Seals	2	2													
S. Elephant Seals		2													
Sperm whales															
Blue Whales	2														
Fin Whales	2														
Minke whales	2														
Humpback whales	2														
Emperor penguins		2													
Gentoo Penguins	2	2													
Chinstrap Penguins	2	2													
Macaroni Penguin	2	2													
Adelie Penguins	2	1													
Flying birds	2	2													
Cephalopods		2	2	2	2	2	2	2			2	2	2	10	10
Other Icefish		2	2	2		2	2						2	2	2
Toothfish							2	2							
Large Nototh		2	2	2		2	2						2	2	2
Small Nototh		2	2	2		2							2	2	2
Shallow Demersals		2	2			2									
Deep demersals Lg.		2	2	2		2		2						2	2
Deep demersals Sm.		2	2	2		2		2						2	2
Myctophids		2	2	2	2	2	2		2	2	2	2			
Other Pelagics		2	2	2	2	2	2		2	2	2	2			
C. gunnari		2	2	2		2								2	2
P. antarcticum		2	2	2	2		2		2	2	2	2	2	2	2
N. gibberifrons		2	2	2		2								2	2
Mollusca			2	2	2		2	2							
Salps			2		2			2						1	1
Urochordata														1	2
Porifera														2	2
Hemichordata								2						2	2
Brachiopoda								2						2	2
Bryozoa								2						2	2
Cnidaria			2					2						2	2
Arth Crustacea			2	2			2	2					2	2	2
Arth Other			2	2											
Worms			2	2				2						2	2
Echinoidea															
Crinoidea															
Ophiuroidea															
Asteroidea															
Holothuroidea								2							
Krill Adult		2	2	2	2	2	2	2	2	2	2	2	2	10	10
Krill Juvenile		2	2	2	2	2	2	2	2	2	2	2	2	10	2
Krill Larvae															
Krill Embryo															
Macro-Zoopl.					2				2	2	2	2		2	2
Micro-Zoopl.					2				2	2	2				
Cryptophytes									2	2	2				
Copepods									2	2	2	2			
Diatoms									2	2	2				
Ice algae									2	2					
Other Phytopl.									2	2	2				
Detritus															

Table Continued on The Next Page

Appendix K. Antarctic Peninsula Model Vulnerabilities

Table K.1 Continued														
Prey predator	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Killer Whales														
Leopard Seal														
Ross Seal														
Weddell Seal														
Crabeater Seal														
Antarctic Fur Seals														
S. Elephant Seals														
Sperm whales														
Blue Whales														
Fin Whales														
Minke whales														
Humpback whales														
Emperor penguins														
Gentoo Penguins														
Chinstrap Penguins														
Macaroni Penguin														
Adelie Penguins			2											
Flying birds			2											
Cephalopods	2	2	2	2	2	2				2	2		2	
Other Icefish	2		2	2	2	2				2	2		2	
Toothfish				2	2		2			2				
Large Nototh	2		2	2	2	2	2			2				
Small Nototh	2		2	2	2	2	2			2	2		2	
Shallow Demersals		2					2			2	2			
Deep demersals Lg.					2	2	2						2	
Deep demersals Sm.	2				2	2	2			2	2		2	
Myctophids	2	2	2	2		2	2				2		2	2
Other Pelagics	2	2	2	2		2	2				2		2	
C. gunnari	2				2	2	2			2				
P. antarcticum	2	2	2	2	2	2	2			2	2		2	
N. gibberifrons	2		2		2	2	2			2				
Mollusca		2	2	2	2	2	2	2	2	2	2	2	2	
Salps			2	2	2	2	2	2	2	2	2	2	2	2
Urochordata				2				2		2	2			
Porifera														
Hemichordata										2				
Brachiopoda													2	
Bryozoa										2	2		2	
Cnidaria			2	2	2	2	2	2		2	2		2	
Arth Crustecea	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Arth Other				2	2	2	2	2	2	2	2			
Worms				2	2	2	2	2	2	2	2	2	2	2
Echinoidea								2						
Crinoidea								2						
Ophiuroidea								2						
Asteroidea								2						
Holothuroidea								2						
Krill Adult	2	1	2	2	2	2	2	2	2	2	2	2	2	2
Krill Juvenile	2	1	2	1	2	2	2	2	2	2	2	2	2	2
Krill Larvae							2	2		2	2			
Krill Embryo							2			2	2			
Macro-Zoopl.		2		2	2		2	2		2	2	2	2	2
Micro-Zoopl.				2	2			2		2	2		2	2
Cryptophytes														
Copepods			2		2			2				2		
Diatoms														
Ice algae							2							
Other Phytopl.							2			2				
Detritus														

Table Continued on The Next Page

Appendix K. Antarctic Peninsula Model Vulnerabilities

Table K.1 Continued														
Prey predator	30	31	32	33	34	35	36	37	38	39	40	41	42	43
Killer Whales														
Leopard Seal														
Ross Seal														
Weddell Seal														
Crabeater Seal														
Antarctic Fur Seals														
S. Elephant Seals														
Sperm whales														
Blue Whales														
Fin Whales														
Minke whales														
Humpback whales														
Emperor penguins														
Gentoo Penguins														
Chinstrap Penguins														
Macaroni Penguin														
Adelie Penguins														
Flying birds														
Cephalopods														
Other Icefish	2													
Toothfish														
Large Nototh														
Small Nototh	2													
Shallow Demersals														
Deep demersals Lg.														
Deep demersals Sm.	2													
Myctophids														
Other Pelagics	2													
C. gunnari														
P. antarcticum	2													
N. gibberifrons	2													
Mollusca	2	2										2	2	2
Salps	2	2								2		2	100	
Urochordata		2										2	2	2
Porifera												2	2	2
Hemichordata														2
Brachiopoda														2
Bryozoa														2
Cnidaria	2	2									2	2	2	2
Arth Crustacea	2	2									2	2	2	2
Arth Other	2	2									2	2	2	2
Worms	2	2	2					2		2	2	2	2	2
Echinoidea								2				2	2	
Crinoidea								2				2	2	2
Ophiuroidea								2				2	2	2
Asteroidea								2				2	2	2
Holothuroidea		2						2			2	2	2	2
Krill Adult	2	2						2						
Krill Juvenile	2	2						2						
Krill Larvae		2						2				2		
Krill Embryo								2				10		2
Macro-Zoopl.	2	2	2	2				2		2	2	2	2	2
Micro-Zoopl.	2	2	2	10	2	2		2	2	2	2	2	2	2
Cryptophytes	2	2	2	10	2	2		2	2	2				
Copepods	2	2	2	2	2			2	2	2	2	2		2
Diatoms	2	2	2	2	2	2		2	2	2			2	2
Ice algae	2	2	2	2	2	2		2	2	2	2			2
Other Phytopl.	2	2	2	2	2	2		2	2	2	2			2
Detritus			2		2	2	2		2	2	2	2	2	2

Table Continued on The Next Page

Appendix K. Antarctic Peninsula Model Vulnerabilities

Table K.1 Continued											
Prey predator	44	45	46	47	48	49	50	51	52	53	55
Killer Whales											
Leopard Seal											
Ross Seal											
Weddell Seal											
Crabeater Seal											
Antarctic Fur Seals											
S. Elephant Seals											
Sperm whales											
Blue Whales											
Fin Whales											
Minke whales											
Humpback whales											
Emperor penguins											
Gentoo Penguins											
Chinstrap Penguins											
Macaroni Penguin											
Adelie Penguins											
Flying birds											
Cephalopods											
Other Icefish											
Toothfish											
Large Nototh											
Small Nototh											
Shallow Demersals											
Deep demersals Lg.											
Deep demersals Sm.											
Myctophids											
Other Pelagics											
C. gunnari											
P. antarcticum											
N. gibberifrons											
Mollusca		2	2								
Salps			2								
Urochordata			2								
Porifera		2	2								
Hemichordata											
Brachiopoda											
Bryozoa	2	2									
Cnidaria		2									
Arth Crustacea	2	2	2								
Arth Other											
Worms	2	2	2								
Echinoidea											
Crinoidea											
Ophiuroidea		2	2								
Asteroidea											
Holothuroidea											
Krill Adult									1		
Krill Juvenile					2				1		
Krill Larvae					1						
Krill Embryo					1.3						
Macro-Zoopl.	2	2	2		2	2					
Micro-Zoopl.	2	2	2		2	2			3		
Cryptophytes		2			10	4.6	2		1	3	
Copepods	2	2	2		2	2			2		
Diatoms		2	2	2	2	2	2		2	2	3
Ice algae		2	2		2	2	2		1	2	2
Other Phytopl.		2	2	2	2	100	2		1	3	3
Detritus	2	2	2	2	2	2		2	2	2	2

Appendix L

Antarctic Peninsula Model Mixed Trophic Impact Values

Appendix L. Antarctic Peninsula Model Mixed Trophic Impact Values

Table L.1: Mixed trophic impacts for the Antarctic Peninsula Model

Impacting	Impacted	1	2	3	4	5	6	7	8	9
1	Killer Whale	-0.31	-0.62	-0.05	-0.34	0.095	0.288	0.575	-0.05	-0.71
2	Leopard seal	-0.12	-0.01	-0.34	-0.12	-0.5	-0.64	-0.85	0.154	0.167
3	Ross seal	0.013	-0.01	-0.01	-0.01	0.002	0.001	0	-0.01	-0.01
4	Weddell Seal	0.107	-0.09	-0.04	-0.08	0.015	0.033	0.049	-0.04	-0.11
5	Crabeater Seal	0.103	-0.08	-0.04	-0.08	-0.06	-0.02	0.042	-0.04	-0.16
6	Antarctic fur seal	0.05	0	-0.06	-0.05	-0.02	-0.03	-0.04	-0.04	-0.05
7	S Elephant seal	0	0.007	-0.01	-0.01	0	-0.01	-0.03	-0.02	0.002
8	Sperm whale	0	0	0	0	0.001	0	-0.01	-0.01	0.001
9	Blue whale	0.001	0	0	0	0	0	0.001	0	0
10	fin whale	0.003	0	0	0	0	0.001	0.003	0	0
11	Minke whale	0.236	-0.22	-0.02	-0.12	0.029	0.096	0.199	-0.02	-0.25
12	Humpback whale	0.048	-0.05	0	-0.02	0.005	0.019	0.041	0	-0.05
13	Emperor penguin	0	0.012	-0.02	-0.01	-0.01	-0.01	-0.02	-0.01	0.003
14	Gentoo Penguin	0.005	0	-0.02	-0.01	0	-0.01	-0.02	-0.03	0
15	Chinstrap penguin	0.012	-0.01	-0.02	-0.01	0.001	0	-0.01	-0.03	-0.01
16	Macaroni Penguin	0.001	0.017	-0.02	-0.01	-0.01	-0.02	-0.03	-0.01	0
17	Adelie Penguin	0	0.065	-0.04	-0.03	-0.06	-0.07	-0.06	0.005	-0.02
18	Flying birds	-0.01	-0.02	-0.05	-0.03	0.006	-0.02	-0.1	-0.12	0
19	Cephalopods	0.012	0.097	0.267	0.129	-0.08	0.048	0.481	0.617	-0.06
20	Other Icefish	0	0.012	-0.01	-0.02	0	-0.02	0.005	0	0.009
21	Toothfish	0	0	0	0	0.001	0	0.013	0.013	0
22	Lg Nototheniidae	0	0.001	0.029	0.012	-0.01	0.01	-0.01	0.001	-0.01
23	Sm Nototheniidae	0	0.007	0	0.001	-0.01	0	-0.01	0	0
24	Shallow demersals	0	0.01	0	0	-0.01	-0.01	-0.01	0.001	0.001
25	Deep demersal lg	0	0.001	0	0	0	0	0	0.003	0.001
26	Deep demersals sm	0	0.005	0	0	0	0	-0.01	0.018	0
27	Myctophids	0	0.006	0.011	0.004	-0.01	0.001	0.066	0	0.044
28	Other pelagics	0	-0.01	-0.05	-0.03	0.004	0	-0.08	-0.1	0.014
29	C. gunni	0	0.003	0.015	0.018	-0.02	0.01	-0.01	0	-0.01
30	P. antarcticum	0.014	-0.01	0.124	0.177	-0.01	-0.02	0.044	0.026	-0.02
31	N. gibberifrons	0	0.003	0.013	0.012	-0.01	0.014	-0.01	-0.01	-0.01
32	Mollusca	0.021	-0.01	0.04	0.175	0.019	-0.01	0.094	0.018	-0.02
33	Salps	0	0.006	0.017	0.001	0.008	0.002	0	0.027	0.003
34	Urochordata	0	0.004	0.01	0.004	0	0.002	0.017	0.023	0
35	Porifera	0	0	0	0	0	0	0	0	0
36	Hemichordata	0	0	0	0	0	0	0	0.004	0
37	Brachiopoda	0	0	0	0	0	0	0	0.004	0
38	Bryozoa	0	0	0	0	0	0	0	0.004	0
39	Cnidaria	0.001	0.001	0.002	0	0.001	0.001	0	0.011	0.002
40	Crustaceans	0.007	0.015	0.047	0.074	-0.02	0.002	0.017	0.011	0
41	Arthropod other	0	0.001	0.006	-0.01	0	0.001	0.004	0.008	0
42	Worms	0.004	0.011	0.006	0	0	0.013	-0.01	0.011	0.011
43	Echinoidea	0	0	0	0	0.001	0	0	0	0
44	Crinoidea	0	0	0	0	0	0	0	0	0
45	Ophiuroidea	-0.01	0.001	-0.01	-0.04	0	0	-0.02	-0.01	0.004
46	Asteroidea	0	0	0	0	0	0	0	0	0
47	Holothuroidea	0	0.001	0.001	0	0	0	0	0.004	0
48	Krill Adult	0.105	0.159	-0.09	-0.1	0.262	0.18	-0.15	0.033	0.263
49	Krill Sub-adult	0.102	0.052	0.003	-0.1	0.189	0.206	-0.01	0.101	0.158
50	Krill juvenile	0	0	0	0	0	0	0	0	0
51	Krill Larvae	0	0	0	0	0	0	0	0	0
52	Macro-zoopl.	-0.05	-0.1	0.066	0.097	-0.16	-0.16	0.136	0	-0.21
53	Micro-zoopl.	0.017	-0.01	0.015	0	0	0.009	0.042	0.035	-0.02
54	Cryptophytes	0.005	-0.01	0.015	0.007	0	-0.01	0.023	0.022	-0.01
55	Copepods	0.022	0.03	-0.02	-0.01	0.05	0.041	-0.04	-0.02	0.069
56	Diatoms	0.037	0.016	0.005	0	0.052	0.042	0.01	0.024	0.051
57	Ice Algae	0.067	0.042	0.002	-0.03	0.116	0.097	0.002	0.061	0.096
58	Other phytopl.	0.01	-0.01	0.028	0.018	-0.01	-0.01	0.044	0.039	-0.02
59	Detritus	0.044	0.016	0.06	0.123	0.042	0.048	0.069	0.063	0.021
	Krill Fishery	0	0	0.001	0.001	0	0	0.001	0	0
	Other Fishery	0	0	0	0	0	0	0	0	0

Table Continued on Next Page

Appendix L. Antarctic Peninsula Model Mixed Trophic Impact Values

Table L.1 Continued											
	Impacting	Impacted	10	11	12	13	14	15	16	17	18
1	Killer Whale		-0.7	-0.7	-0.71	0.6	0.329	0.158	0.5	0.32	0
2	Leopard seal		0.162	0.139	0.175	-0.9	-0.66	-0.51	-0.82	-0.52	0.017
3	Ross seal		-0.01	-0.01	-0.01	0.006	0	0	0.006	0.006	0
4	Weddell Seal		-0.11	-0.1	-0.1	0.068	0.029	0.001	0.067	0.049	0
5	Crabeater Seal		-0.16	-0.13	-0.17	0.022	0.009	-0.02	0.008	-0.03	-0.02
6	Antarctic fur seal		-0.05	-0.05	-0.05	-0.01	-0.04	-0.04	-0.02	0	-0.01
7	S Elephant seal		0.002	0.002	0.003	-0.01	-0.01	-0.01	-0.01	0	0
8	Sperm whale		0.001	0	0.001	0	0	-0.01	0.001	0.002	0
9	Blue whale		0	0	0	0.001	0	0	0	0	0
10	fin whale		0	0	0	0.003	0.002	0.001	0.002	0.001	0
11	Minke whale		-0.25	-0.24	-0.25	0.204	0.114	0.055	0.169	0.107	0
12	Humpback whale		-0.05	-0.05	-0.05	0.041	0.023	0.011	0.034	0.021	0
13	Emperor penguin		0.003	0.003	0.003	-0.02	-0.02	-0.01	-0.01	-0.01	0
14	Gentoo Penguin		0	0	0	0	-0.03	-0.03	0	0.003	0
15	Chinstrap penguin		-0.01	-0.01	-0.01	0.004	-0.02	-0.03	0.002	0.006	0
16	Macaroni Penguin		0	0	0	-0.02	-0.03	-0.02	-0.03	-0.01	0
17	Adelie Penguin		-0.02	-0.01	-0.03	-0.09	-0.06	-0.05	-0.08	-0.08	-0.01
18	Flying birds		0	0.003	0	-0.01	-0.03	-0.04	-0.01	-0.17	-0.51
19	Cephalopods		-0.05	-0.02	-0.04	-0.01	0.163	0.225	-0.03	-0.1	0.078
20	Other Icefish		0.008	0.005	0.008	-0.01	-0.04	-0.02	-0.01	0	0.007
21	Toothfish		0	0	0	0	0	0	0	0.002	0
22	Lg Nototheniidae		-0.01	0	-0.01	0.017	0.023	0.019	0.031	-0.01	-0.01
23	Sm Nototheniidae		0	0	0	0.017	0.028	0.001	0.006	-0.02	0.005
24	Shallow demersals		0.001	0.002	0.002	-0.01	-0.01	-0.01	-0.01	0	0
25	Deep demersals lg		0.001	0	0.001	0	0.002	0.002	0	0	0
26	Deep demersals sm		0	0	0	-0.01	0.024	0.025	0	0	0
27	Myctophids		0.045	0	0.005	-0.01	-0.01	-0.01	0.009	-0.01	0.006
28	Other pelagics		0.014	0.008	0.004	-0.03	-0.03	-0.04	0.004	0.009	-0.01
29	C. gunni		-0.01	-0.01	-0.01	-0.01	0	0.001	0.005	-0.02	0
30	P. antarcticum		-0.01	-0.03	-0.04	0.185	0.009	0.018	-0.01	0.019	0
31	N. gibberifrons		-0.01	0	-0.01	-0.01	0.056	0.023	0.001	-0.01	-0.01
32	Mollusca		-0.02	-0.03	-0.03	0.021	0.001	0	0.001	0.068	0.014
33	Salps		0	-0.01	0.004	0	0.018	0.019	0	-0.01	0.026
34	Urochordata		0	0	0	0	0.025	0.027	0	-0.01	0.003
35	Porifera		0	0	0	0	0.008	0.018	0	0	0
36	Hemichordata		0	0	0	0	0.019	0.019	0	0	0
37	Brachiopoda		0	0	0	0	0.014	0.014	0	0	0
38	Bryozoa		0	0	0	0	0.014	0.014	0	0	0
39	Cnidaria		0.001	0.001	0.002	0	0.025	0.025	0.001	0.001	0.001
40	Crustaceans		0	-0.01	-0.01	0.009	0.029	0.011	0.032	0.025	0.035
41	Arthropod other		0	0.002	0.001	0	-0.01	0	0	-0.01	0
42	Worms		0.008	0.003	0.011	0.009	0.003	0.002	0.011	0.003	-0.01
43	Echinoidea		0	0	0.001	0	-0.01	-0.01	0	0	0
44	Crinoidea		0	0	0	0	0	0	0	0	0
45	Ophiuroidea		0.003	0.005	0.007	-0.01	-0.01	-0.01	0	-0.02	-0.01
46	Asteroidea		0	0	0	0	0	0	0	0	0
47	Holothuroidea		0	0	0	0	0	0	0	0	0
48	Krill Adult		0.24	0.02	0.339	0.102	0.056	0.06	0.173	0.491	0.1
49	Krill Sub-adult		0.054	0.158	0.149	0.112	-0.1	-0.09	0.181	-0.11	0.068
50	Krill juvenile		0	0	0	0	0	0	0	0	0
51	Krill Larvae		0	0	0	0	0	0	0	0	0
52	Macro-zoopl.		-0.13	-0.01	-0.2	-0.06	0.106	0.097	-0.13	-0.12	-0.07
53	Micro-zoopl.		-0.01	0.054	-0.03	0.018	0.01	0.011	0.008	-0.01	0.002
54	Cryptophytes		0.009	0.014	-0.02	0.003	0.028	0.027	0	0	0.007
55	Copepods		0.057	0.004	0.082	0.039	-0.03	-0.03	0.043	0.073	0.034
56	Diatoms		0.073	0.044	0.054	0.047	0.021	0.02	0.045	0.067	0.034
57	Ice Algae		0.08	0.075	0.111	0.072	0.036	0.035	0.094	0.107	0.049
58	Other phytopl.		0.004	0.027	-0.03	0.008	0.051	0.048	0	-0.01	0.009
59	Detritus		0.001	0.018	0.009	0.049	0.036	0.03	0.064	0.031	0.041
	Krill Fishery		0	0	0	0	0	0	0	0	0
	Other Fishery		0	0	0	0	0	0	0	0	0

Table Continued on Next Page

Appendix L. Antarctic Peninsula Model Mixed Trophic Impact Values

Table L.1 Continued										
Impacting	Impacted	19	20	21	22	23	24	25	26	27
1	Killer Whale	-0.06	-0.06	-0.11	-0.14	-0.01	-0.06	-0.08	-0.05	0
2	Leopard seal	0.183	0.134	0.136	0.327	0	0.044	0.223	0.129	0.009
3	Ross seal	-0.02	-0.01	0.005	-0.02	0.003	0	0	0	0.001
4	Weddell Seal	-0.06	-0.02	0.002	-0.09	0	0.014	-0.03	-0.02	-0.01
5	Crabeater Seal	-0.04	-0.01	0.003	0	0.018	0.031	0	0.004	-0.03
6	Antarctic fur seal	-0.06	-0.08	0.006	-0.12	0.004	-0.04	-0.03	0	0.013
7	S Elephant seal	-0.02	0.008	-0.19	0.008	0.008	0	0.006	0.001	-0.02
8	Sperm whale	-0.01	0.011	-0.1	0.004	0.005	0.008	-0.04	-0.01	0.004
9	Blue whale	0	0	0	0	0	0	0	0	0
10	fin whale	0	0	0	0	0	0	0	0	0
11	Minke whale	-0.02	-0.02	-0.04	-0.05	0	-0.02	-0.03	-0.02	0.002
12	Humpback whale	-0.01	0	-0.01	-0.01	0	0	-0.01	0	0
13	Emperor penguin	-0.02	-0.01	0.007	-0.03	-0.01	0.007	0.009	0.008	0.009
14	Gentoo Penguin	-0.03	-0.02	0.022	-0.05	-0.01	0.066	-0.18	-0.09	0.018
15	Chinstrap penguin	-0.04	-0.01	0.031	-0.04	0.011	0.056	-0.18	-0.09	0.016
16	Macaroni Penguin	-0.01	-0.05	-0.01	-0.14	-0.01	0.028	0.03	-0.02	0
17	Adelie Penguin	0.009	0.011	0.009	0.023	0.004	-0.35	0.009	0.008	-0.02
18	Flying birds	-0.16	-0.13	0.054	0.014	-0.11	0.045	0.044	0	-0.08
19	Cephalopods	-0.16	-0.05	-0.5	-0.09	-0.1	0.066	-0.07	0	-0.19
20	Other Icefish	0	-0.1	0.092	-0.11	-0.05	0.102	-0.16	-0.07	0.03
21	Toothfish	0	-0.07	-0.02	-0.01	-0.02	0	0	0	0
22	Lg Nototheniidae	0.005	0.022	0.033	-0.09	-0.09	-0.13	-0.1	-0.08	-0.09
23	Sm Nototheniidae	-0.01	0.005	0.138	-0.01	-0.04	-0.05	0.022	0.04	-0.02
24	Shallow demersals	0.001	0	0	0	-0.01	-0.02	0.02	0	-0.01
25	Deep demersals lg	0	-0.01	-0.09	-0.03	0	-0.19	-0.01	-0.14	0.01
26	Deep demersals sm	0	-0.09	-0.02	0.008	-0.07	-0.14	0.069	-0.05	-0.03
27	Myctophids	0	-0.01	0	0.007	-0.02	-0.03	-0.01	0.026	-0.03
28	Other pelagics	-0.12	-0.08	0.07	0.043	-0.05	0	-0.07	0.033	-0.1
29	C. gunni	0	0.027	0.051	-0.01	0	0.009	0.011	-0.01	-0.02
30	P. antarcticum	0.045	-0.04	-0.04	-0.03	-0.04	-0.05	0.04	-0.06	-0.03
31	N. gibberifrons	-0.01	0.144	0.079	-0.06	-0.04	-0.05	-0.04	-0.05	-0.01
32	Mollusca	-0.01	-0.02	-0.03	0.001	0.038	-0.04	0.139	0.099	0.212
33	Salps	0.009	0.012	0.009	0.021	0	0.016	-0.01	0.009	0
34	Urochordata	0.032	0	-0.02	-0.01	0.003	0	0.009	0	-0.01
35	Porifera	0	0	0.001	0	0	0	-0.01	0	0
36	Hemichordata	0	0	0	0	0	0.001	0	0	0.001
37	Brachiopoda	0	0	0.001	0	0	0.002	-0.01	0	0
38	Bryozoa	0	0	0.001	0	0	0.003	-0.01	0.003	0
39	Cnidaria	0	0.019	0.006	-0.01	0.004	0	0.004	-0.01	0
40	Crustaceans	0.015	0.033	0.129	0.199	0.216	0.558	0.051	0.141	0.145
41	Arthropod other	0.017	0	-0.01	0.001	-0.04	-0.01	-0.02	-0.02	-0.02
42	Worms	0.014	0.016	0.027	0.036	0.128	0	0.021	0.042	-0.03
43	Echinoidea	0	0	0	-0.01	-0.01	-0.02	0.001	0	0
44	Crinoidea	0	0	0	0	0.001	0	0	0	0
45	Ophiuroidea	0	0	-0.01	-0.02	-0.04	-0.04	-0.03	-0.03	-0.05
46	Asteroidea	0	0	0	0	0	0	0	0	0
47	Holothuroidea	0.002	0.002	0.004	0.004	0.012	0.011	0	0.001	0
48	Krill Adult	-0.03	0.091	0.098	0.053	0	-0.18	0.031	0.009	0.006
49	Krill Sub-adult	0.109	0.023	-0.08	-0.09	-0.19	-0.24	-0.03	-0.12	-0.31
50	Krill juvenile	0	0	0	0	0	0	0.01	0.003	0
51	Krill Larvae	0	0	0	0	0	0	0	0	0
52	Macro-zoopl.	0.036	0.004	-0.02	0.04	0.139	0.245	0.005	0.09	0.155
53	Micro-zoopl.	0.05	0.012	-0.03	-0.03	0.001	-0.01	0	-0.01	-0.03
54	Cryptophytes	0.021	0.011	-0.01	0.003	0.011	0.018	0	0.01	0.007
55	Copepods	-0.03	0.003	0.031	-0.01	-0.01	-0.04	0	-0.01	0.13
56	Diatoms	0.019	0.023	0.006	-0.01	0.008	-0.02	0.006	0.004	0.091
57	Ice Algae	0.055	0.055	0	0.037	-0.02	-0.08	0.007	-0.01	-0.03
58	Other phytopl.	0.039	0.022	-0.01	0.043	0.015	0.017	0.023	0.007	0.015
59	Detritus	0.045	0.027	0.049	0.109	0.178	0.248	0.101	0.127	0.116
	Krill Fishery	0	0	0	0	0	0.001	0	0	0
	Other Fishery	0	0	0	0	0	0	0	0	0

Table Continued on Next Page

Appendix L. Antarctic Peninsula Model Mixed Trophic Impact Values

Table L.1 Continued										
Impacting	Impacted	28	29	30	31	32	33	34	35	36
1	Killer Whale	-0.01	-0.09	0.023	-0.03	-0.01	0.007	0.01	-0.01	-0.2
2	Leopard seal	0.049	0.269	0	0.076	0.017	-0.02	-0.03	0.007	0.453
3	Ross seal	0	-0.01	0	0	0	0.002	0.004	0	0.001
4	Weddell Seal	0	-0.08	-0.05	-0.02	-0.01	0.011	0.013	-0.01	-0.02
5	Crabeater Seal	-0.04	-0.05	-0.03	0.012	0	-0.02	0	0.008	0.027
6	Antarctic fur seal	-0.02	-0.21	0.041	-0.05	0	0.011	0.014	0	0.037
7	S Elephant seal	0	0.007	0.01	0	0	0.003	0.006	0	0.009
8	Sperm whale	0	0.001	0.007	0	0	0.001	0.004	0	-0.02
9	Blue whale	0	0	0	0	0	0	0	0	0
10	fin whale	0	0	0	0	0	0	0	0	0
11	Minke whale	-0.01	-0.04	0.007	-0.01	0.001	0.002	0.003	0.001	-0.06
12	Humpback whale	0	-0.01	0.002	0	0	0	0	0	-0.01
13	Emperor penguin	0.006	0.013	-0.02	0.015	0.003	0.004	0.004	0	0.01
14	Gentoo Penguin	0.006	-0.01	0.017	-0.06	0	0.004	0.003	0	-0.39
15	Chinstrap penguin	0.004	-0.01	0.018	-0.03	0	0.004	0.004	0	-0.37
16	Macaroni Penguin	0	-0.06	0.012	0.003	0.001	0.005	0.002	0	0.019
17	Adelie Penguin	-0.04	0	-0.04	0.011	-0.01	0	-0.01	0	0.042
18	Flying birds	-0.1	0.038	0.063	0.037	-0.01	-0.02	0.037	0.001	0.034
19	Cephalopods	0.036	-0.03	-0.37	0.072	0.091	-0.09	-0.21	0.018	-0.15
20	Other Icefish	0.026	-0.26	-0.02	-0.37	0.003	0.002	0.009	-0.01	0.03
21	Toothfish	0	0	0.002	0.018	0	0.001	0.001	0	0
22	Lg Nototheniidae	-0.09	-0.1	-0.02	-0.06	0.005	-0.02	0.005	0.006	-0.01
23	Sm Nototheniidae	0.008	-0.01	-0.01	-0.03	-0.02	-0.01	-0.01	0.011	-0.01
24	Shallow demersals	0	0.003	0	-0.01	0	0	0	0.001	0.005
25	Deep demersals lg	0.009	-0.02	0	0.001	0	0.002	0	0	-0.05
26	Deep demersals sm	-0.04	0.025	-0.01	0.036	0	0	0	0	-0.02
27	Myctophids	0.02	0.006	-0.01	-0.01	-0.05	-0.02	0	0	0.01
28	Other pelagics	-0.07	0.026	-0.04	0.048	0	-0.01	0.03	0	0.034
29	C. gunni	0	-0.03	0.002	-0.02	0.005	-0.01	0	0.003	0.005
30	P. antarcticum	-0.1	-0.03	-0.09	-0.2	-0.13	-0.05	-0.01	0.023	0.037
31	N. gibberifrons	0.001	-0.06	0.001	-0.11	0.001	0	-0.01	0.014	-0.02
32	Mollusca	0.015	-0.03	0.093	-0.04	-0.05	0.068	0.034	0.055	-0.04
33	Salps	0.036	0.023	-0.01	0	0	-0.06	-0.03	0	-0.02
34	Urochordata	0.001	0	-0.02	0.009	0	-0.01	-0.02	0	-0.02
35	Porifera	0	0	0	0	-0.02	-0.01	-0.01	-0.03	-0.03
36	Hemichordata	0	0	0.001	0	0	0	0	0	-0.02
37	Brachiopoda	0.005	0	0	0	0	0	0	0	-0.01
38	Bryozoa	0.004	0	0	0	0	0	0	0	-0.01
39	Cnidaria	0.011	-0.01	0	0	0	-0.09	0.004	0	-0.03
40	Crustaceans	0.003	-0.04	0.051	0.263	-0.02	0.048	0.044	-0.04	-0.04
41	Arthropod other	0	0	-0.01	-0.02	-0.06	0.022	-0.2	0.027	0.008
42	Worms	-0.01	0.006	0.002	0.081	-0.08	-0.39	-0.26	-0.42	0.048
43	Echinoidea	0	0.002	0	-0.01	0.005	0.017	0.01	-0.04	-0.1
44	Crinoidea	0	0	0	0	0	0.001	0	0.001	0.001
45	Ophiuroidea	-0.01	0.009	-0.02	-0.02	-0.18	0.04	0.02	-0.13	0.005
46	Asteroidea	0	0	0	0	0.002	-0.01	-0.03	-0.01	0
47	Holothuroidea	0	0	0	0.014	-0.02	0	-0.03	-0.01	-0.01
48	Krill Adult	0.073	0.334	-0.08	0.03	0.019	0.031	0.044	0.043	-0.01
49	Krill Sub-adult	0.048	0.252	0.035	-0.12	-0.31	0.088	0.045	-0.31	-0.49
50	Krill juvenile	0	0	0	0.001	0	0	0	0	0
51	Krill Larvae	0	0	0	0	0	0.001	0	0	0
52	Macro-zoopl.	-0.03	-0.29	0.033	0.069	0.103	-0.25	-0.16	0.05	0.149
53	Micro-zoopl.	0.012	0	0	-0.02	-0.02	-0.05	-0.07	-0.04	-0.03
54	Cryptophytes	0.016	-0.01	0	0.011	0.015	0.296	0.11	0.01	-0.01
55	Copepods	-0.01	0.077	0.091	-0.03	-0.06	-0.09	-0.11	-0.01	0
56	Diatoms	0.013	0.055	0.067	-0.01	-0.02	0.023	0.071	-0.02	-0.05
57	Ice Algae	0.036	0.116	0.022	0.027	-0.05	0.007	0.108	-0.07	-0.16
58	Other phytopl.	0.019	-0.03	0.004	0.045	0.042	0.346	0.26	0.004	-0.04
59	Detritus	0.022	0.013	0.091	0.147	0.421	-0.11	-0.06	0.484	0.756
	Krill Fishery	0	0	0	0	0	0	0	0	0.001
	Other Fishery	0	0	0	0	0	0	0	0	0

Table Continued on Next Page

Appendix L. Antarctic Peninsula Model Mixed Trophic Impact Values

Table L.1 Continued										
Impacting	Impacted	37	38	39	40	41	42	43	44	45
1	Killer Whale	-0.09	-0.02	0.003	0.017	0.018	0.003	0	-0.01	0
2	Leopard seal	0.197	0.041	-0.01	-0.06	-0.06	-0.01	0.001	0.016	0
3	Ross seal	0.001	0	0	0.002	0.004	0	0	0	0
4	Weddell Seal	-0.01	-0.01	0.001	0.01	0.014	0	0	-0.01	0
5	Crabeater Seal	0.022	-0.01	0.021	0.03	0.018	0.014	0.005	0.005	0.006
6	Antarctic fur seal	0.022	-0.01	0.008	0.02	0.016	0.002	0	-0.01	0
7	S Elephant seal	0.006	0	0.001	0	0.005	0	0	0	0
8	Sperm whale	-0.01	0	0	0	0.003	0	0	0	0
9	Blue whale	0	0	0	0	0	0	0	0	0
10	fin whale	0	0	0	0	0	0	0	0	0
11	Minke whale	-0.03	-0.01	0.003	0.01	0.008	0.003	0.001	0	0.001
12	Humpback whale	-0.01	0	0.001	0.002	0.002	0.001	0	0	0
13	Emperor penguin	0.003	0	0.001	0.004	0.006	0	0.001	0	0
14	Gentoo Penguin	-0.18	-0.02	-0.01	0.01	0.007	0	0	0	0
15	Chinstrap penguin	-0.18	-0.01	-0.01	0.004	0.008	0	0	-0.01	0
16	Macaroni Penguin	0.009	0	0.003	0.01	0.007	0.001	0.001	0	0.001
17	Adelie Penguin	0.034	0.001	0.011	0	0	0.004	0	0	0
18	Flying birds	0.053	0.002	0.003	-0.01	0.036	0.008	0	0.006	0
19	Cephalopods	-0.09	0.012	-0.04	0.02	-0.17	-0.01	0.022	0.082	0.016
20	Other Icefish	0.002	-0.02	-0.03	0.055	0.002	0	0	0.004	0
21	Toothfish	0	0	0.002	0	0	0	0	0.002	0
22	Lg Nototheniidae	0.024	0.022	0.014	-0.05	-0.02	0.004	0	0.022	0
23	Sm Nototheniidae	-0.01	0.03	0	-0.06	0.007	0	0	-0.13	0.001
24	Shallow demersals	0.003	0.008	0.005	-0.02	0	0.003	0	0.001	0
25	Deep demersals lg	0	0	-0.01	0.007	0.001	0	0	0	0
26	Deep demersals sm	0.002	0	0.004	-0.01	0	0	0	0.009	0
27	Myctophids	0	0.012	0.008	-0.04	0.001	0.013	-0.01	0.003	-0.01
28	Other pelagics	-0.3	-0.02	-0.03	0	0.031	0	0	-0.01	0
29	C. gunni	0.002	0	0.003	0.008	0.003	0.002	0.003	0.003	0.002
30	P. antarcticum	0.049	0.031	0.023	-0.04	-0.06	0.049	-0.02	0.051	0
31	N. gibberifrons	-0.01	0.035	-0.01	-0.1	0	0	0	0.011	0.001
32	Mollusca	-0.05	0.001	0.022	-0.04	0.081	-0.18	0.154	-0.03	0.103
33	Salps	-0.03	-0.01	0.064	-0.01	0	0.01	-0.02	0	-0.01
34	Urochordata	-0.01	-0.01	-0.01	0	0.037	0.001	0.004	-0.01	0
35	Porifera	-0.02	-0.01	-0.01	0	0	0.012	0.032	-0.02	0.009
36	Hemichordata	-0.01	0	0	0	0	0	0	0	0
37	Brachiopoda	-0.01	0	0	0	0	0	0.002	0	0
38	Bryozoa	-0.01	-0.01	0	0.003	0.008	0	0.008	0.119	0.002
39	Cnidaria	-0.02	0	-0.02	0.001	0.008	-0.01	0.014	-0.01	0.005
40	Crustaceans	-0.04	-0.27	-0.18	-0.16	-0.1	-0.1	0.104	0.001	0.041
41	Arthropod other	-0.01	-0.1	-0.06	-0.03	-0.11	-0.07	0.056	-0.28	0.032
42	Worms	0.214	-0.03	-0.14	-0.02	-0.12	-0.11	-0.79	-0.07	-0.33
43	Echinoidea	-0.27	-0.04	-0.04	-0.02	-0.06	-0.03	0.015	-0.17	0.001
44	Crinoidea	0	-0.07	0.001	0	0.001	0	0.002	-0.01	0
45	Ophiuroidea	-0.01	-0.08	-0.1	-0.05	0.001	-0.06	0.05	0	-0.23
46	Asteroidea	0	0.003	0.004	0	0.026	-0.01	0.012	-0.01	-0.04
47	Holothuroidea	-0.01	-0.02	-0.01	0.014	0.097	0	0.035	-0.05	0
48	Krill Adult	-0.05	0.04	-0.14	-0.05	0.014	-0.01	-0.01	0.02	0.016
49	Krill Sub-adult	-0.13	0.068	-0.1	-0.36	-0.21	-0.22	-0.13	-0.24	-0.19
50	Krill juvenile	0	0	0	0	0.004	0	0	0	0
51	Krill Larvae	0	0	0.001	0	0.001	0	0.001	0	0
52	Macro-zoopl.	0.084	-0.15	0.476	0.29	0.075	0.2	0.045	0.076	0.052
53	Micro-zoopl.	-0.03	-0.06	0.055	-0.02	0.007	0.019	-0.02	-0.01	0.007
54	Cryptophytes	0.031	0.116	0.081	0.014	0.016	0.019	0.002	0.017	0.028
55	Copepods	-0.08	-0.09	-0.12	-0.01	-0.02	-0.04	0.028	-0.02	-0.02
56	Diatoms	-0.01	0.095	0.037	0	-0.01	0.003	0.026	-0.01	0.002
57	Ice Algae	-0.02	0.123	0.113	-0.05	-0.04	-0.03	0.003	-0.04	-0.02
58	Other phytopl.	0.312	0.123	0.152	0.021	0.024	0.023	0.058	0.008	0.028
59	Detritus	0.144	-0.02	-0.17	0.363	0.206	0.256	0.12	0.368	0.254
	Krill Fishery	0	0	0.001	0.001	0	0	0	0	0
	Other Fishery	0	0	0	0	0	0	0	0	0

Table Continued on Next Page

Appendix L. Antarctic Peninsula Model Mixed Trophic Impact Values

Table L.1 Continued										
Impacting	Impacted	46	47	48	49	50	51	52	53	54
1	Killer Whale	-0.01	-0.01	-0.04	0.002	0.004	0	0.011	0	0
2	Leopard seal	0.016	0.026	0.107	0.012	-0.01	-0.01	-0.04	0.003	0.005
3	Ross seal	0	0	0.001	0.002	0	0	0	0	0
4	Weddell Seal	-0.01	-0.01	0.001	0.008	0	-0.01	0	0	0
5	Crabeater Seal	0.005	0.004	-0.11	-0.03	0.004	0.04	0.048	0.009	-0.01
6	Antarctic fur seal	0	-0.01	-0.01	0	0	-0.01	0.003	0	0
7	S Elephant seal	0	0	0.002	0.001	0	0	0	0	0
8	Sperm whale	0	0	0	0	0	0	0	0	0
9	Blue whale	0	0	0	0	0	0	0	0	0
10	fin whale	0	0	0	0	0	0	0	0	0
11	Minke whale	0	0	-0.02	-0.01	0.002	0.005	0.008	0.001	0
12	Humpback whale	0	0	-0.01	0	0.001	0.001	0.002	0	0
13	Emperor penguin	0	0	0	0.002	0	-0.01	0	0	0
14	Gentoo Penguin	0	-0.01	0	0.002	0.011	0	0	0	0
15	Chinstrap penguin	0	0	0	0.002	0.007	0	0	0	0
16	Macaroni Penguin	0	0	0	0	0.002	0	0.001	0	0
17	Adelie Penguin	0	0	-0.06	0.004	0.004	0.013	0.017	0	0
18	Flying birds	-0.01	0	-0.01	-0.01	-0.02	-0.01	0.008	0.005	0
19	Cephalopods	0.075	0.059	-0.03	-0.03	0.129	0.12	0.022	0.022	0.002
20	Other Icefish	0	-0.02	0.007	0.005	0.031	-0.01	-0.01	0	0.001
21	Toothfish	0	0	0.001	0	0	0	0	0	0
22	Lg Nototheniidae	0.008	0.023	-0.01	0	-0.01	0.019	0.007	0.002	0
23	Sm Nototheniidae	0	0.016	-0.01	0	-0.03	0	0.006	0.001	0
24	Shallow demersals	0	0.006	0	0	0.001	0.001	0	0	0
25	Deep demersals lg	0	0	0.001	0.001	-0.03	0.001	0	0	0
26	Deep demersals sm	0	0.001	0	0.001	-0.04	-0.02	0	0	0
27	Myctophids	-0.01	0.008	-0.01	0	0	0.006	0.004	0.002	0.001
28	Other pelagics	-0.01	-0.01	-0.01	0.005	-0.02	-0.02	0.002	0	0
29	C. gunni	0.003	0.002	-0.02	-0.01	0.003	0.01	0.011	0.003	0
30	P. antarcticum	0.026	0.056	-0.01	-0.06	0.062	0.086	0.025	0.029	0
31	N. gibberifrons	0.004	0.028	-0.01	-0.01	-0.04	0.01	0.01	0.001	0
32	Mollusca	0.066	0.038	-0.02	-0.02	-0.06	-0.09	0.02	-0.02	-0.01
33	Salps	0	0	0.003	0.006	0	0.001	-0.02	-0.13	-0.05
34	Urochordata	0	-0.01	0	0	-0.03	-0.02	0	-0.01	0
35	Porifera	0	-0.02	0.001	0	0.002	-0.02	0	0.001	0
36	Hemichordata	0	0	0	0	0	0	0	0	0
37	Brachiopoda	0	0	0	0	0	0	0	0	0
38	Bryozoa	0	0	0	0	-0.01	-0.01	0	0	0
39	Cnidaria	0	0	0.003	0.004	-0.01	-0.01	-0.01	0.011	0.008
40	Crustaceans	0.086	-0.19	-0.01	0	0.036	0.034	-0.02	0.002	0
41	Arthropod other	-0.25	-0.18	0	0	-0.6	-0.5	0.007	0	0.001
42	Worms	-0.47	-0.33	0.023	0.019	0.067	0.156	-0.08	0.051	0.044
43	Echinoidea	-0.03	-0.02	0	0	0.041	-0.14	0.001	0	0
44	Crinoidea	0.001	0.001	0	0	0	0	0	0	0
45	Ophiuroidea	0.067	0.04	0.002	0.001	0.005	-0.01	0.003	-0.01	0
46	Asteroidea	-0.01	-0.01	0	0	-0.02	-0.02	0	0.001	0.001
47	Holothuroidea	-0.04	-0.04	0	0	-0.07	-0.07	0	0.001	0
48	Krill Adult	0.017	0.05	-0.03	-0.05	-0.12	-0.22	-0.29	0.07	0.012
49	Krill Sub-adult	-0.24	-0.31	-0.12	-0.15	0.057	-0.4	-0.32	-0.33	0.093
50	Krill juvenile	0	0	0	0	-0.01	0	0	0	0
51	Krill Larvae	0	0	0	0	0	-0.01	0	0	0
52	Macro-zoopl.	0.076	0.045	-0.34	-0.38	-0.02	0.272	0.203	-0.1	-0.18
53	Micro-zoopl.	0.009	-0.02	-0.01	0.005	-0.08	-0.02	-0.04	-0.15	-0.39
54	Cryptophytes	0.009	0	-0.01	-0.03	0.012	0.007	0.092	0.11	-0.11
55	Copepods	-0.01	0	0.162	0.046	-0.18	-0.06	-0.25	-0.15	-0.14
56	Diatoms	0	-0.03	0.127	0.037	-0.11	-0.06	0.036	0.053	0.155
57	Ice Algae	-0.03	-0.09	0.207	0.166	0.601	-0.16	0.154	0.022	0.082
58	Other phytopl.	0.03	0	-0.03	-0.04	0.166	0	0.151	0.244	0.037
59	Detritus	0.336	0.522	-0.03	0.178	-0.19	0.673	-0.05	-0.02	0.095
	Krill Fishery	0	0	-0.01	0	0.001	0.002	0.002	0	0
	Other Fishery	0	0	0	0	0	0	0	0	0

Table Continued on Next Page

Appendix L. Antarctic Peninsula Model Mixed Trophic Impact Values

Table L.1 Continued								
Impacting	Impacted	55	56	57	58	59	Krill Fishery	Other Fishery
1	Killer Whale	0.006	0	0	0	0	-0.03	-0.05
2	Leopard seal	-0.03	0.018	-0.01	0.007	-0.01	0.083	0.111
3	Ross seal	0	0.001	0	0	0	0.001	0
4	Weddell Seal	-0.01	0.003	0	0.001	-0.01	0.003	-0.03
5	Crabeater Seal	0.04	-0.03	0.011	-0.01	0.024	-0.09	-0.01
6	Antarctic fur seal	0.003	0	0.001	0	0.002	-0.01	-0.05
7	S Elephant seal	0	0.001	0	0	0	0.002	-0.02
8	Sperm whale	0	0	0	0	0	0	-0.01
9	Blue whale	0	0	0	0	0	0	0
10	fin whale	0	0	0	0	0	0	0
11	Minke whale	0.007	-0.01	0.002	0	0.005	-0.02	-0.02
12	Humpback whale	0.002	0	0	0	0.001	-0.01	0
13	Emperor penguin	0	0	0	0	0	0	0
14	Gentoo Penguin	0	0.001	0	0	0	0	-0.01
15	Chinstrap penguin	0	0.001	0	0	0	0	0
16	Macaroni Penguin	0.001	0	0.001	0	0.001	0	-0.03
17	Adelie Penguin	0.009	-0.01	0	0	0	-0.04	0
18	Flying birds	0.005	0	0.002	0	0.005	-0.01	-0.02
19	Cephalopods	0.025	-0.02	0.009	-0.01	0.02	-0.03	-0.14
20	Other Icefish	0	0.002	0	0.001	0	0.007	0.027
21	Toothfish	0	0	0	0	0	0.001	0.1
22	Lg Nototheniidae	0.004	0	0.001	0	0.003	-0.01	0.058
23	Sm Nototheniidae	0.003	0	0.001	0	0.003	-0.01	0.115
24	Shallow demersals	0	0	0	0	0	0	0
25	Deep demersals lg	0	0	0	0	0	0.001	-0.02
26	Deep demersals sm	0	0	0	0	0	0	-0.02
27	Myctophids	0.002	0	0	0	0.002	-0.01	0.106
28	Other pelagics	0	0	0	0	0	-0.01	0.093
29	C. gunni	0.009	-0.01	0.003	0	0.006	-0.02	0.112
30	P. antarcticum	0.034	-0.02	0.018	-0.01	0.049	-0.02	0.046
31	N. gibberifrons	0.006	0	0.002	0	0.006	-0.01	0.105
32	Mollusca	0.011	-0.01	0.005	-0.01	-0.02	-0.02	0.028
33	Salps	0	0.005	0.004	0	0	0.004	0.01
34	Urochordata	0	0	0	0	0	0	0
35	Porifera	0.001	0	0.001	0	-0.02	0	0
36	Hemichordata	0	0	0	0	0	0	0
37	Brachiopoda	0	0	0	0	0	0	0
38	Bryozoa	0	0	0	0	0	0	0.001
39	Cnidaria	0	0.002	0	0.002	0	0.004	0.003
40	Crustaceans	0.002	0	0.003	0	-0.01	-0.01	0.111
41	Arthropod other	0.001	0	0.002	0.002	0.01	0	-0.01
42	Worms	-0.01	0.008	0	0.017	-0.04	0.022	0.029
43	Echinoidea	0	0	0	0	0.002	0	0
44	Crinoidea	0	0	0	0	0	0	0
45	Ophiuroidea	0	0.001	0	0.002	0.002	0.002	-0.02
46	Asteroidea	0	0	0	0	0	0	0
47	Holothuroidea	0.001	0	0.001	0	-0.01	0	0.004
48	Krill Adult	-0.17	0.118	0	0.039	0.034	0.714	0.067
49	Krill Sub-adult	-0.42	0.229	-0.23	0.112	-0.58	0.121	-0.05
50	Krill juvenile	0	0	0	0	0	0	0
51	Krill Larvae	0	0	0	0	0	0	0
52	Macro-zoopl.	0.241	-0.16	0.06	-0.12	0.237	-0.35	0.012
53	Micro-zoopl.	-0.02	-0.01	-0.02	-0.23	-0.02	-0.01	-0.01
54	Cryptophytes	0.01	-0.01	0.001	-0.06	0.014	-0.01	0.004
55	Copepods	-0.43	-0.43	-0.19	-0.09	-0.02	0.133	0.031
56	Diatoms	0.381	-0.3	-0.15	-0.14	-0.03	0.104	0.027
57	Ice Algae	0.01	-0.04	-0.12	-0.07	-0.13	0.197	0.027
58	Other phytopl.	0.042	-0.04	-0.01	-0.12	0.014	-0.03	0.013
59	Detritus	-0.09	0.047	-0.05	0.01	0	0.02	0.084
	Krill Fishery	0.001	0	0	0	0	0	0
	Other Fishery	0	0	0	0	0	0	0

Appendix M

Antarctic Peninsula Monte Carlo CV Values

Appendix M. Antarctic Peninsula Monte Carlo CV Values

Table M.1: Monte Carlo CV values used for the Antarctic Peninsula model

	Group name	Biomass	P/B	Q/B	Diet
1	Killer Whales	0.7	0.5	0.5	1
2	Leopard Seal	0.7	0.5	0.5	1
3	Ross Seal	0.4	0.5	0.5	0.2
4	Weddell Seal	0.7	0.5	0.5	1
5	Crabeater Seal	0.7	0.5	0.5	1
6	Antarctic Fur Seals	0.7	0.5	0.5	1
7	S Elephant Seals	0.7	0.5	0.5	0.7
8	Sperm whales	0.7	0.5	0.5	0.5
9	Blue Whales	0.7	0.5	0.5	0.7
10	Fin Whales	0.7	0.5	0.5	0.7
11	Minke whales	0.7	0.5	0.5	0.7
12	Humpback whales	0.7	0.5	0.5	0.7
13	Emperor penguins	0	0.7	0.5	0.7
14	Gentoo Penguins	0.7	0.5	0.5	0.7
15	Chinstrap Penguins	0.7	0.5	0.5	0.7
16	Macaroni Penguin	0	0.5	0.5	0.5
17	Adelie Penguins	0.7	1	0.5	0.7
18	Flying birds	0.4	0.8	0.8	0.2
19	Cephalopods	0.4	0.2	0.2	0.2
20	Other Icefish	0.7	0.5	0.5	0.5
21	Toothfish	0.7	0.5	0.5	0.5
22	Large Nototheniidae	0.7	0.5	0.5	0.5
23	Small Nototheniidae	0.7	0.5	0.5	0.5
24	Shallow Demersals	0.7	0.5	0.5	0.5
25	Deep demersals Large	0.7	0.5	0.5	1
26	Deep demersals Small	0.7	0.5	0.5	1
27	Myctophids	0.7	0.5	0.5	0.5
28	Other Pelagics	0.7	0.5	0.5	0.5
29	C. gunnari	0.7	0.5	0.5	0.5
30	P. antarcticum	0.7	0.5	0.5	0.5
31	N. gibberifrons	0.7	0.5	0.5	0.5
32	Mollusca	1	0.2	0.2	0.5
33	Salps	1	0.8	0.8	0.5
34	Urochordata	1	0.2	0.2	0.5
35	Porifera	1	0.2	0.2	0.5
36	Hemichordata	1	0.2	0.2	0.5
37	Brachiopoda	1	0.2	0.2	0.5
38	Bryozoa	1	0.2	0.2	0.5
39	Cnidaria	1	0.2	0.2	0.5
40	Crustaceans	1	0.2	0.2	0.5
41	Other Arthropods	1	0.2	0.2	0.5
42	Worms	1	0.2	0.2	0.5
43	Echinoidea	1	0.2	0.2	0.5
44	Crinoidea	1	0.2	0.2	0.5
45	Ophiuroidea	1	0.2	0.2	0.5
46	Asteroidea	1	0.2	0.2	0.5
47	Holothuroidea	1	0.2	0.2	0.5
48	Krill Adult	1	0.8	1	1
49	Krill Juvenile	1	0.8	0.5	1
50	Krill Larvae	1	0.8	0.5	1
51	Krill Embryo	1	0.8	0.5	1
52	Macro-Zoopl.	0.7	0	0	0.2
53	Micro-Zoopl.	0.7	0	0	0.2
54	Cryptophytes	0.7	-	-	-
55	Copepods	0.4	0.6	0.6	0.7
56	Diatoms	0.7	-	-	-
57	Ice algae	0.7	-	-	-
58	Other Phytoplankton	0.4	-	-	-

Appendix N

Antarctic Peninsula Monte Carlo Results

Appendix N. Antarctic Peninsula Monte Carlo Results

Table N.1: Monte Carlo results for Biomass ($t \cdot km^{-2}$), P/B (y^{-1}), Ecotrophic Efficiency (EE), and Biomass Accumulation ($t \cdot km^{-2} \cdot y^{-1}$)

		Biomass			P/B		
	Group name	Lower	Mean	Upper	Lower	Mean	Upper
1	Killer Whales	0.001	0.001	0.001	0.025	0.050	0.075
2	Leopard Seal	0.004	0.006	0.007	0.060	0.120	0.180
3	Ross Seal	0.002	0.004	0.006	0.065	0.130	0.195
4	Weddell Seal	0.015	0.021	0.027	0.085	0.170	0.255
5	Crabeater Seal	0.115	0.164	0.213	0.045	0.090	0.135
6	Antarctic Fur Seals	0.020	0.028	0.037	0.088	0.175	0.263
7	S Elephant Seals	0.005	0.006	0.008	0.083	0.165	0.248
8	Sperm whales	0.004	0.005	0.007	0.017	0.034	0.051
9	Blue Whales	0.000	0.001	0.001	0.016	0.032	0.048
10	Fin Whales	0.002	0.003	0.004	0.018	0.035	0.053
11	Minke whales	0.046	0.065	0.085	0.032	0.064	0.096
12	Humpback whales	0.014	0.020	0.026	0.020	0.040	0.060
13	Emperor penguins	0.001	0.005	0.009	0.105	0.150	0.195
14	Gentoo Penguins	0.005	0.007	0.008	0.110	0.220	0.330
15	Chinstrap Penguins	0.004	0.005	0.007	0.165	0.330	0.495
16	Macaroni Penguin	0.003	0.014	0.024	0.150	0.300	0.450
17	Adelie Penguins	0.024	0.034	0.044	0.261	0.290	0.319
18	Flying birds	0.095	0.190	0.285	0.272	0.340	0.408
19	Cephalopods	1.245	2.490	3.735	0.380	0.950	1.520
20	Other Icefish	0.236	0.337	0.438	0.190	0.380	0.570
21	Toothfish	0.032	0.046	0.060	0.083	0.165	0.248
22	Large Nototheniidae	0.413	0.590	0.767	0.185	0.370	0.555
23	Small Nototheniidae	0.239	0.341	0.443	0.325	0.650	0.975
24	Shallow Demersals	0.022	0.031	0.040	0.375	0.750	1.125
25	Deep demersals Lg	0.029	0.042	0.055	0.145	0.290	0.435
26	Deep demersals Sm	0.056	0.080	0.104	0.325	0.650	0.975
27	Myctophids	0.130	0.185	0.241	0.675	1.350	2.025
28	Other Pelagics	0.343	0.490	0.637	0.275	0.550	0.825
29	C. gunnari	0.203	0.290	0.377	0.240	0.480	0.720
30	P. antarcticum	0.875	1.250	1.625	0.550	1.100	1.650
31	N. gibberifrons	0.567	0.810	1.053	0.205	0.410	0.615
32	Mollusca	8.550	9.500	10.450	0.256	0.639	1.022
33	Salps	2.250	2.500	2.750	2.400	3.000	3.600
34	Urochordata	4.545	5.050	5.555	0.094	0.234	0.374
35	Porifera	11.447	12.719	13.991	0.064	0.159	0.254
36	Hemichordata	0.041	0.045	0.050	0.150	0.375	0.600
37	Brachiopoda	0.025	0.028	0.030	0.359	0.898	1.437
38	Bryozoa	0.442	0.491	0.540	0.190	0.475	0.760
39	Cnidaria	1.378	1.531	1.684	0.100	0.250	0.400
40	Crustaceans	3.252	3.613	3.974	0.420	1.050	1.680
41	Arthropod Other	0.909	1.010	1.111	0.246	0.616	0.985
42	Worms	10.800	12.000	13.200	0.280	0.700	1.120
43	Echinoidea	3.897	4.330	4.763	0.046	0.116	0.186
44	Crinoidea	0.147	0.164	0.180	0.050	0.125	0.200
45	Ophiuroidea	6.084	6.760	7.436	0.180	0.450	0.720
46	Asteroidea	1.600	1.778	1.956	0.092	0.231	0.370
47	Holothuroidea	4.905	5.450	5.995	0.126	0.316	0.505
48	Krill Adult	8.172	9.080	9.988	1.200	1.500	1.800
49	Krill Juvenile	23.303	25.893	28.482	0.720	0.900	1.080
50	Krill Larvae	0.011	0.013	0.014	2.000	2.500	3.000
51	Krill Embryo	0.003	0.003	0.004	6.400	8.000	9.600
52	Macro-Zooplankton	5.719	8.170	10.621	1.615	8.073	14.531
53	Micro-Zooplankton	1.456	2.080	2.704	5.400	27.000	48.600
54	Cryptophytes	1.260	1.800	2.340	60.000	75.000	90.000
55	Copepods	10.940	21.880	32.820	10.306	17.177	24.048
56	Diatoms	12.187	17.410	22.633	72.408	90.510	108.612
57	Ice algae	17.500	25.000	32.500	36.000	45.000	54.000
58	Other Phytoplankton	2.750	5.500	8.250	84.000	105.000	126.000

Table Continued on Next Page

Appendix N. Antarctic Peninsula Monte Carlo Results

Table N.1 Continued							
Biomass				P/B			
EE				BA			
	Group name	Lower	Mean	Upper	Lower	Mean	Upper
1	Killer Whales	0.000	0.000	0.000	0.000	0.000	0.000
2	Leopard Seal	0.509	0.637	0.764	-0.001	0.000	0.001
3	Ross Seal	0.664	0.830	0.996	0.000	0.000	0.000
4	Weddell Seal	0.551	0.689	0.827	-0.002	0.000	0.002
5	Crabeater Seal	0.290	0.363	0.435	-0.016	0.000	0.016
6	Antarctic Fur Seals	0.690	0.862	1.000	-0.003	0.000	0.003
7	S Elephant Seals	0.349	0.437	0.524	-0.001	0.000	0.001
8	Sperm whales	0.000	0.000	0.000	-0.001	0.000	0.001
9	Blue Whales	0.546	0.683	0.820	0.000	0.000	0.000
10	Fin Whales	0.419	0.524	0.629	0.000	0.000	0.000
11	Minke whales	0.728	0.910	1.000	-0.007	0.000	0.007
12	Humpback whales	0.770	0.963	1.000	-0.002	0.000	0.002
13	Emperor penguins	0.746	0.933	1.000	-0.001	0.000	0.001
14	Gentoo Penguins	0.514	0.642	0.771	0.000	0.000	0.001
15	Chinstrap Penguins	0.556	0.696	0.835	0.000	0.001	0.001
16	Macaroni Penguin	0.298	0.373	0.447	-0.001	0.000	0.001
17	Adelie Penguins	0.635	0.793	0.952	-0.003	0.000	0.003
18	Flying birds	0.760	0.950	1.000	-0.019	0.000	0.019
19	Cephalopods	0.522	0.653	0.784	-0.249	0.000	0.249
20	Other Icefish	0.581	0.726	0.871	-0.034	0.000	0.034
21	Toothfish	0.502	0.627	0.752	-0.005	0.000	0.005
22	Large Nototheniidae	0.362	0.452	0.543	-0.059	0.000	0.059
23	Small Nototheniidae	0.699	0.873	1.000	-0.034	0.000	0.034
24	Shallow Demersals	0.290	0.362	0.434	-0.003	0.000	0.003
25	Deep demersals Lg	0.642	0.803	0.964	-0.004	0.000	0.004
26	Deep demersals Sm	0.656	0.820	0.984	-0.008	0.000	0.008
27	Myctophids	0.706	0.883	1.000	-0.019	0.000	0.019
28	Other Pelagics	0.670	0.838	1.000	-0.049	0.000	0.049
29	C. gunnari	0.380	0.475	0.571	-0.029	0.000	0.029
30	P. antarcticum	0.483	0.603	0.724	-0.125	0.000	0.125
31	N. gibberifrons	0.516	0.645	0.774	-0.081	0.000	0.081
32	Mollusca	0.436	0.545	0.654	-0.950	0.000	0.950
33	Salps	0.167	0.209	0.251	-0.250	0.000	0.250
34	Urochordata	0.443	0.554	0.665	-0.505	0.000	0.505
35	Porifera	0.652	0.815	0.979	-1.272	0.000	1.272
36	Hemichordata	0.428	0.534	0.641	-0.005	0.000	0.005
37	Brachiopoda	0.472	0.590	0.708	-0.003	0.000	0.003
38	Bryozoa	0.760	0.950	1.000	-0.049	0.000	0.049
39	Cnidaria	0.786	0.982	1.000	-0.153	0.000	0.153
40	Crustaceans	0.711	0.888	1.000	-0.361	0.000	0.361
41	Arthropod Other	0.784	0.981	1.000	-0.101	0.000	0.101
42	Worms	0.675	0.844	1.000	-1.200	0.000	1.200
43	Echinoidea	0.619	0.774	0.929	-0.433	0.000	0.433
44	Crinoidea	0.419	0.523	0.628	-0.016	0.000	0.016
45	Ophiuroidea	0.441	0.551	0.661	-0.676	0.000	0.676
46	Asteroidea	0.619	0.774	0.928	-0.178	0.000	0.178
47	Holothuroidea	0.750	0.938	1.000	-0.545	0.000	0.545
48	Krill Adult	0.554	0.693	0.831	-0.908	0.000	0.908
49	Krill Juvenile	0.634	0.792	0.950	-2.589	0.000	2.589
50	Krill Larvae	0.636	0.795	0.954	-0.001	0.000	0.001
51	Krill Embryo	0.369	0.461	0.554	0.000	0.000	0.000
52	Macro-Zooplankton	0.760	0.950	1.000	-0.817	0.000	0.817
53	Micro-Zooplankton	0.745	0.931	1.000	-0.208	0.000	0.208
54	Cryptophytes	0.560	0.700	0.840	-0.180	0.000	0.180
55	Copepods	0.760	0.950	1.000	-2.188	0.000	2.188
56	Diatoms	0.397	0.497	0.596	-1.741	0.000	1.741
57	Ice algae	0.735	0.919	1.000	-2.500	0.000	2.500
58	Other Phytoplankton	0.660	0.825	0.989	-0.550	0.000	0.550

Appendix O

Antarctic Peninsula Monte Carlo Graphs

Appendix O. Antarctic Peninsula Monte Carlo Graphs

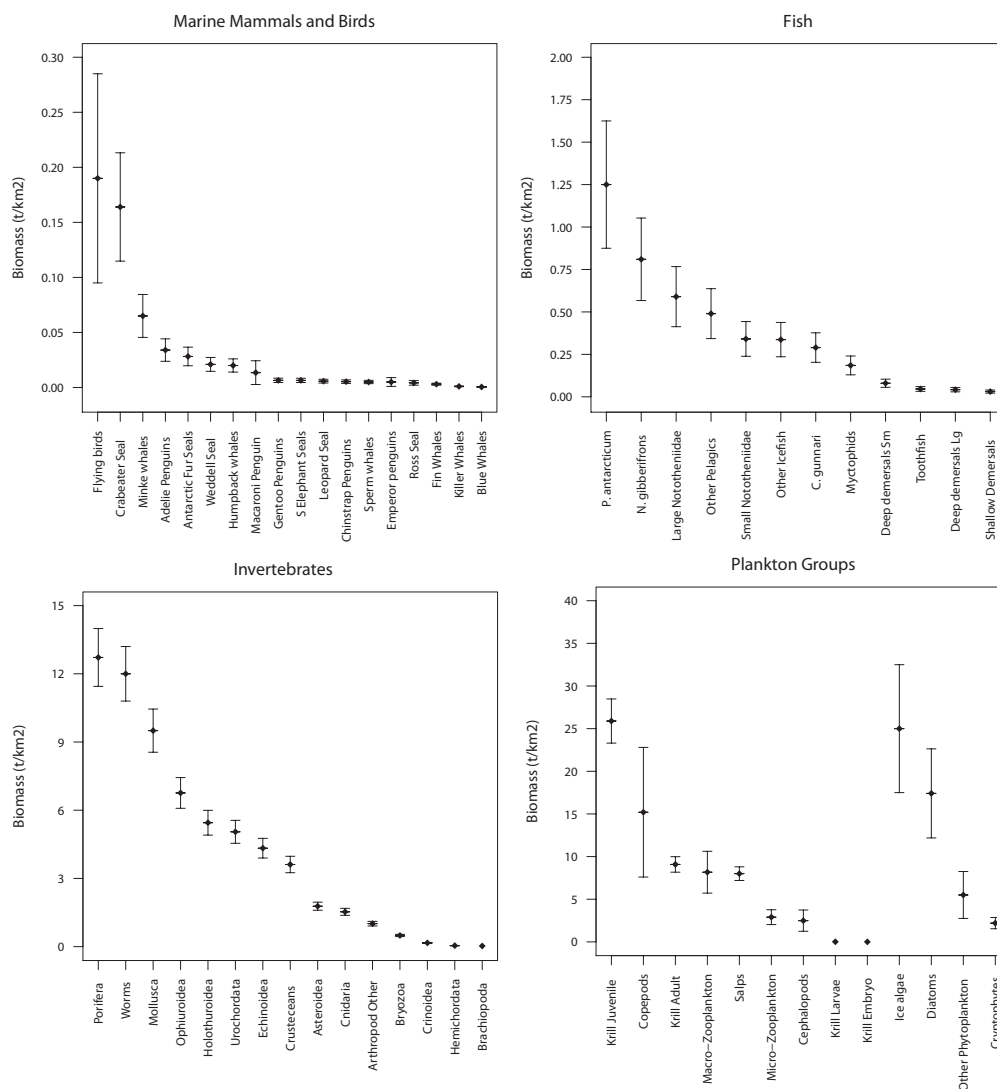


Figure O.1: Mean and 95% CI for Monte Carlo biomass results as presented in $t \cdot km^{-2}$ from 1000 simulations. CV values presented in appendix M.

Appendix P

Antarctic Peninsula Model Biomass Trends By Species

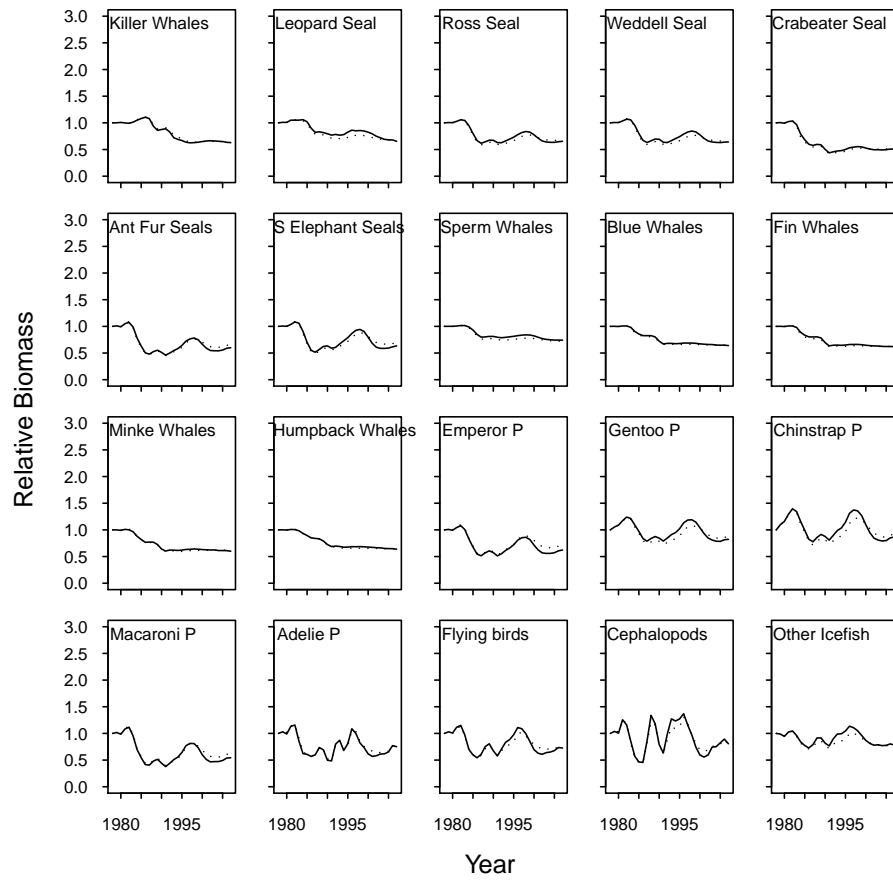
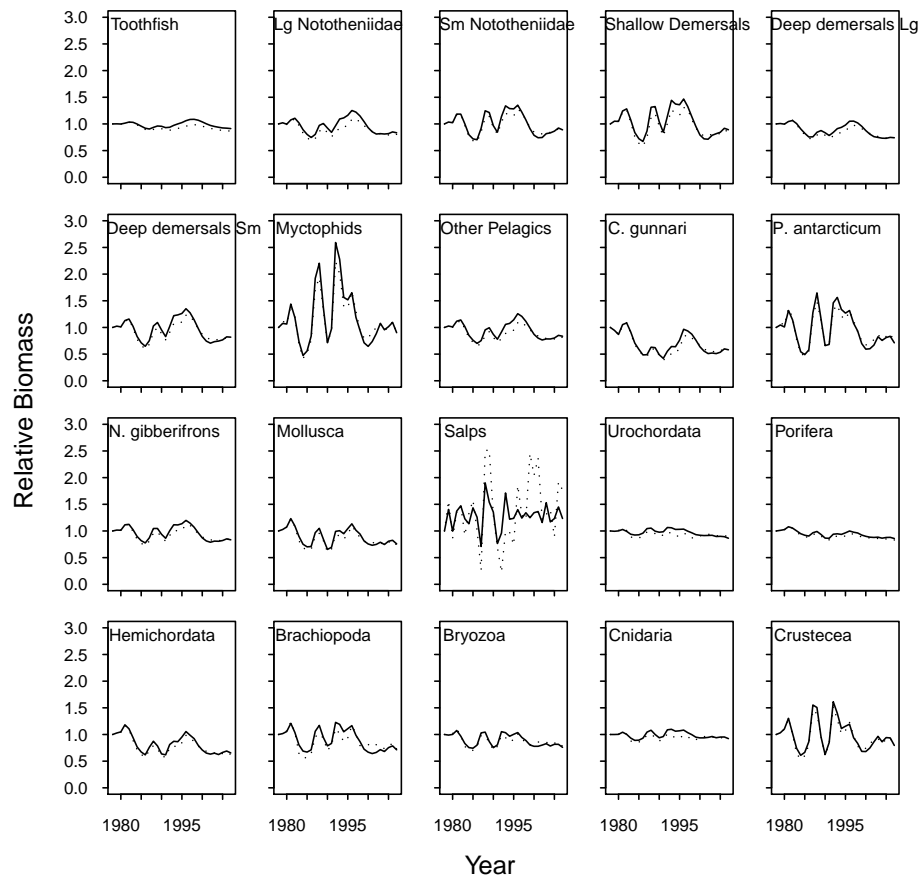
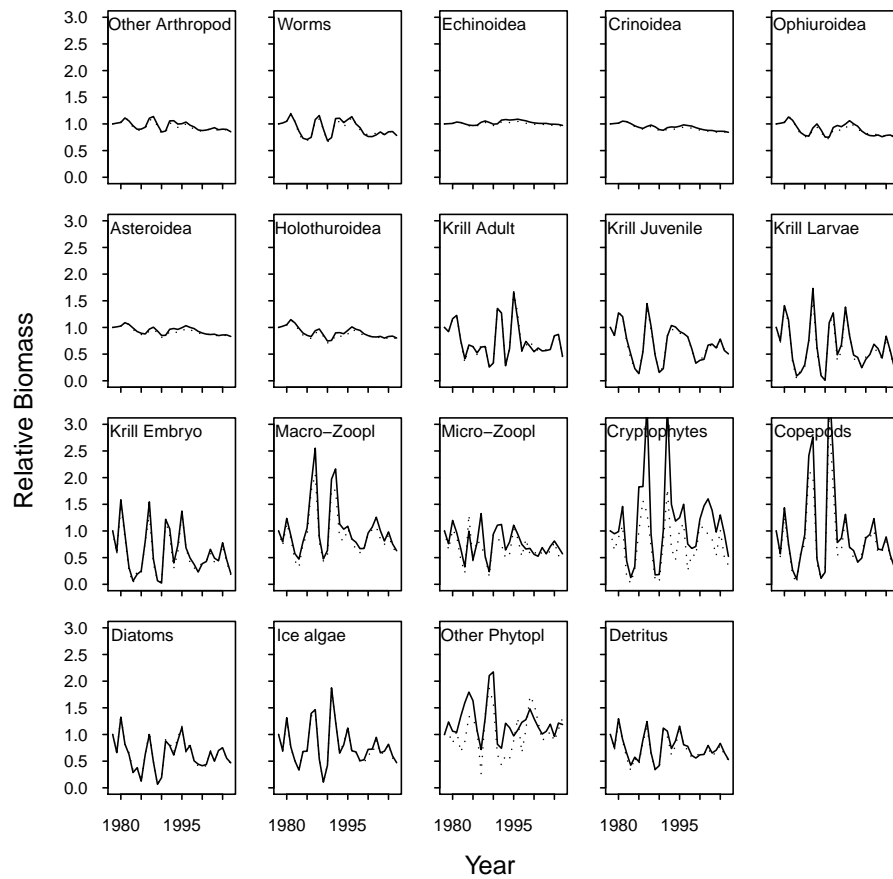


Figure P.1: Biomass trends for the SST (solid lines) and SOI (dotted lines) fitted models.

Appendix P. Antarctic Peninsula Model Biomass Trends By Species



Biomass trends for the SST (solid lines) and SOI (dotted lines) fitted models.



Biomass trends for the SST (solid lines) and SOI (dotted lines) fitted models.